# RESEARCH IN PLANT TRANSPIRATION: 1961

**Production Research Report No. 70**



**Agricultural Research Service**

**U.S. DEPARTMENT OF AGRICULTURE**

**For**

**Meteorology Department**

**U.S. Army Electronic Proving Ground**

## USAEPG SUMMARY

DA Task: 3A99–27–005–08
Title: Research in Plant Transpiration: 1961
Originator: Soil and Water Conservation Research Division, Agricultural Research Service, U.S. Department of Agriculture, Watkinsville, Ga.

The broad objective of this research is to evaluate the role of plants as a factor in the transfer of water from the soil to the atmosphere. Water is lost as vapor from living plants through a process known as transpiration. Generally, the leaves are the principal sites of transpiration. Although water may be lost to some extent from any part of the leaf surface, most of the transpiration occurs through pores of variable size called stomates. Two processes are involved in stomatal transpiration: (1) evaporation of water from cell wall surfaces within the leaf; and (2) diffusion of the water vapor from intercellular spaces through the stomates into the atmosphere. The rate of transpiration is a function of the number of open stomates and their respective perimeters, both of which depend upon the configuration of the adjacent guard cells. The research included studies of three types.

(1) A series of experiments was carried out in the controlled environment growth room to evaluate the effect of radiant energy, temperature, humidity, and other environmental factors on plant transpiration. Prediction equations for transpiration were developed from data obtained in extensive tests of one species. Although subject to some limitations, the data obtained by the equations account for about 80 percent of the variability in transpiration during the period of the experiments. Results of these experiments indicate that temperature has an indirect positive effect upon transpiration in that it increases the vapor pressure deficit (v.p.d.) (vapor pressure of water at the leaf temperature minus the vapor pressure of water in the air surrounding the plant). However, the direct effect of temperature upon transpiration appears to be negative for values above 30° C. Further studies with other species show a close relation between soil moisture and transpiration rates.

(2) Studies were undertaken to investigate the basic causes of stomatal action. It is generally agreed that stomates open or close in accordance with swelling or shrinking of the adjacent guard cells. The changes have been considered to depend upon the starch-sugar equilibrium and the resulting variation in osmotic pressure. In a test of this hypothesis, sugar content in guard and epidermal cells was monitored for periods up to 36 hours during which guard cells were operable. Cellular studies showed that guard cells have extraordinary ability to remain operative under adverse conditions.

(3) Foliar sprays (three growth-regulators, an alcohol, and a wax) were tested for possible effects on transpiration. No material tested was outstanding in suppressing transpiration of the several plant species in the test.

This report contains no general conclusions or recommendations.

Meteorology Department
USAEPG

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This study was conducted under Interdepartmental Cross Service Order No. 3–59, dated 24 February 1959, which is authorized in letter OCSigO, SIGRD–8b–5, dated 13 August 1957, "Proposed Coordinated Signal Corps Meteorological Program."

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U.S. DEPARTMENT OF AGRICULTURE
For
Meteorology Department
U.S. ARMY ELECTRONIC PROVING GROUND
Fort Huachuca, Ariz.



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# RESEARCH IN PLANT TRANSPIRATION: 1961

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## INTRODUCTION

The objective of this research on plant transpiration is to evaluate the role of plants as a factor in the hydrologic cycle. Specifically, the objectives are:

(1) To measure the effects of radiant energy, temperature, humidity, and other environmental factors on transpiration.

(2) To develop better methods and techniques for measuring transpiration.

(3) To gain knowledge of the cellular processes and factors that control or affect guard cell action.

(4) To observe and to measure accurately the reactions of guard cells.

(5) To discover and to evaluate chemical, genetic, physical, and other means to control transpiration.

(6) To develop instruments and equipment that will aid in fulfilling the above-listed objectives.

Moisture is transmitted from the land surface to the atmosphere by the process of evapotranspiration. Evaporation of moisture from a nonvegetated soil surface accounts for a part of this moisture transfer and is controlled by micrometeorological and soil factors. Where vegetation is present the biologic properties of the plant, as influenced by the environment, control the transfer of water from the soil to the atmosphere. Transpiration is largely controlled by plants through manipulation of the guard cells surrounding the stomatal openings in the leaves.

An understanding of the mechanism of stomatal opening and closing and of the reaction of plants to certain external stimuli will permit the development of control procedures and will ultimately lead to increased water use efficiency.

Before undertaking research on transpiration, it was necessary to develop and put into operation several scientific instruments. During the first year of research (1960), a high light-intensity plant growth room, $CO_2$ and $H_2O$ mixing and monitoring systems, leaf chambers, stomata camera, and an instrument for measuring light quality were developed at the Southern Piedmont Soil Conservation Field Station.

The characteristics and capabilities of a high light-intensity, controlled-environment growth room was reported by USAEPG (*35*).[1] Normal plants were produced in the growth room. Preliminary experiments showed an increase in transpiration rate with increasing temperature, radiant energy, vapor pressure deficit, and soil moisture availability.

Preliminary cellular studies by tissue culture methods, to probe the mechanism of guard cell operation and the effects of foliar application of two growth regulators on transpiration, were also described.

## CONTROLLED ENVIRONMENT STUDIES

### EFFECT OF CONTAINER SIZE ON TRANSPIRATION

In studies of environmental effects on transpiration under growth room conditions, the confinement of roots to a given area of soil poses certain restrictions on water availability. In other words, much less soil is available and, therefore, less water may be available to the plant than under field conditions. The container in which the plants are grown must be small enough to move about for weighing and determining the leaf area, but even more important, the size of container must not seriously affect the transpirational pattern. Initial studies by Williams and coworkers (*35*) determined that 46-ounce juice cans were optimum size for growth room use, but no evaluation of the effect of the container size on transpiration was made. A study was initiated to compare the transpiration of plants grown in 46-ounce cans with that of those grown in 92-ounce cans—the latter containing approximately twice the amount of soil.

[1] Italic numbers in parentheses refer to Literature Cited, p. 29.

## Procedure

*Phaseolus vulgaris* L. variety Red Kidney bean seeds were germinated in auxiliary growth chambers, and a uniform population transferred to the growth room at emergence. The plants were grown at 25° C. and approximately 50 percent relative humidity for 3 weeks prior to the experimental period. Light intensity was about 0.42 cal. cm.$^{-2}$ min.$^{-1}$ the first week of growth and 0.82 cal. cm.$^{-2}$ min.$^{-1}$ thereafter and during the experimental period. The ambient temperature remained at 25° and relative humidity at 50 percent for the first 2 days, with a relative humidity of 80 percent for the third and fourth day. The plants were watered by subirrigation at 1700 the night preceding the test and drained at 2200. White polyethylene sheeting was placed around each plant and over the top of the can to prevent evaporation of moisture from the soil surface.

The next morning, beginning at 0800, water loss was measured by weighing the containers at hourly intervals during the period that lights were on. The period of low humidity (fig. 1) was terminated when the plants were visibly wilted. Then the plants were reirrigated and

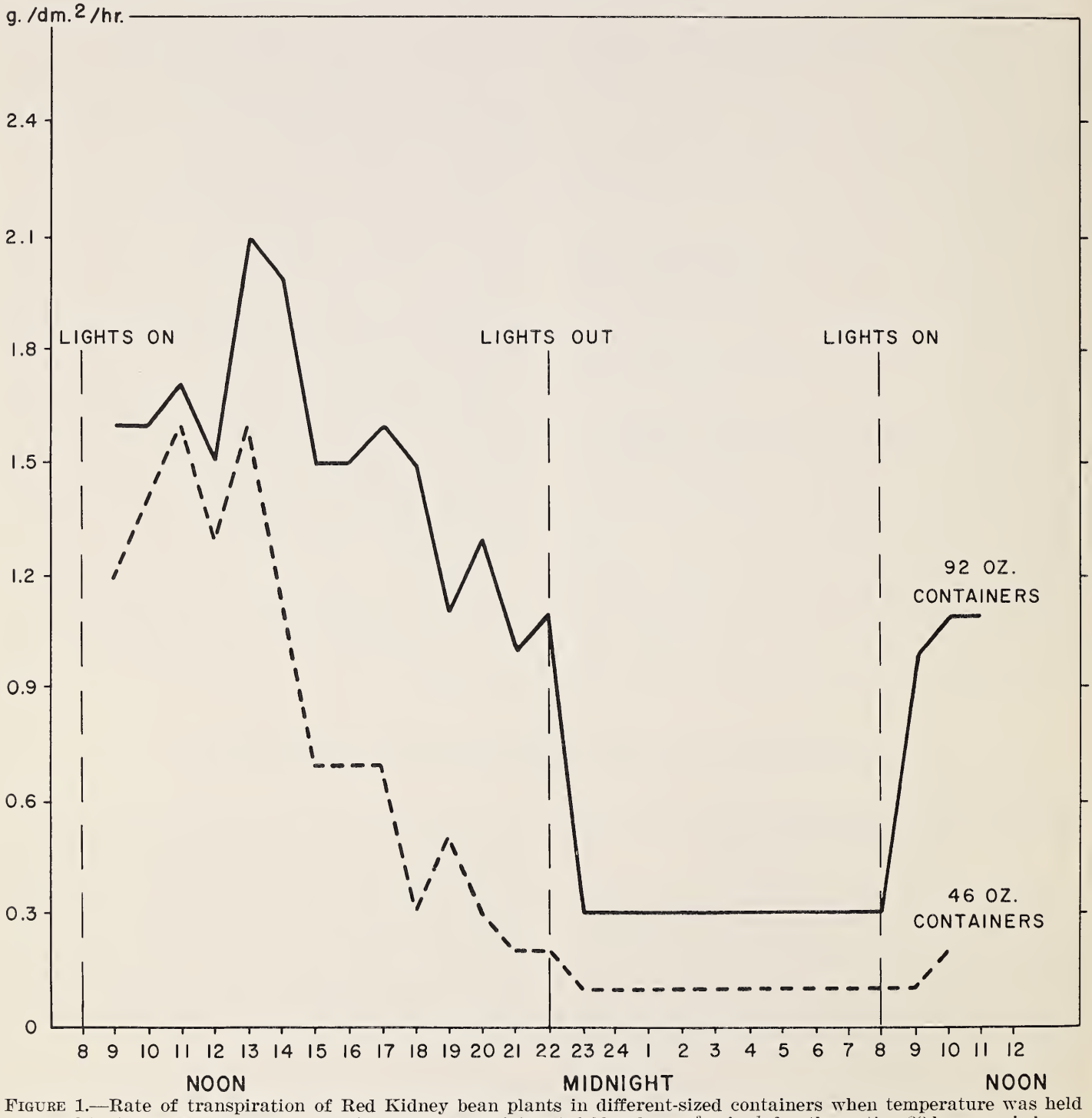


FIGURE 1.—Rate of transpiration of Red Kidney bean plants in different-sized containers when temperature was held at 25° C., relative humidity at 50 percent, and light at 0.82 cal. cm.$^{-2}$ min.$^{-1}$ for the entire 28-hour period.

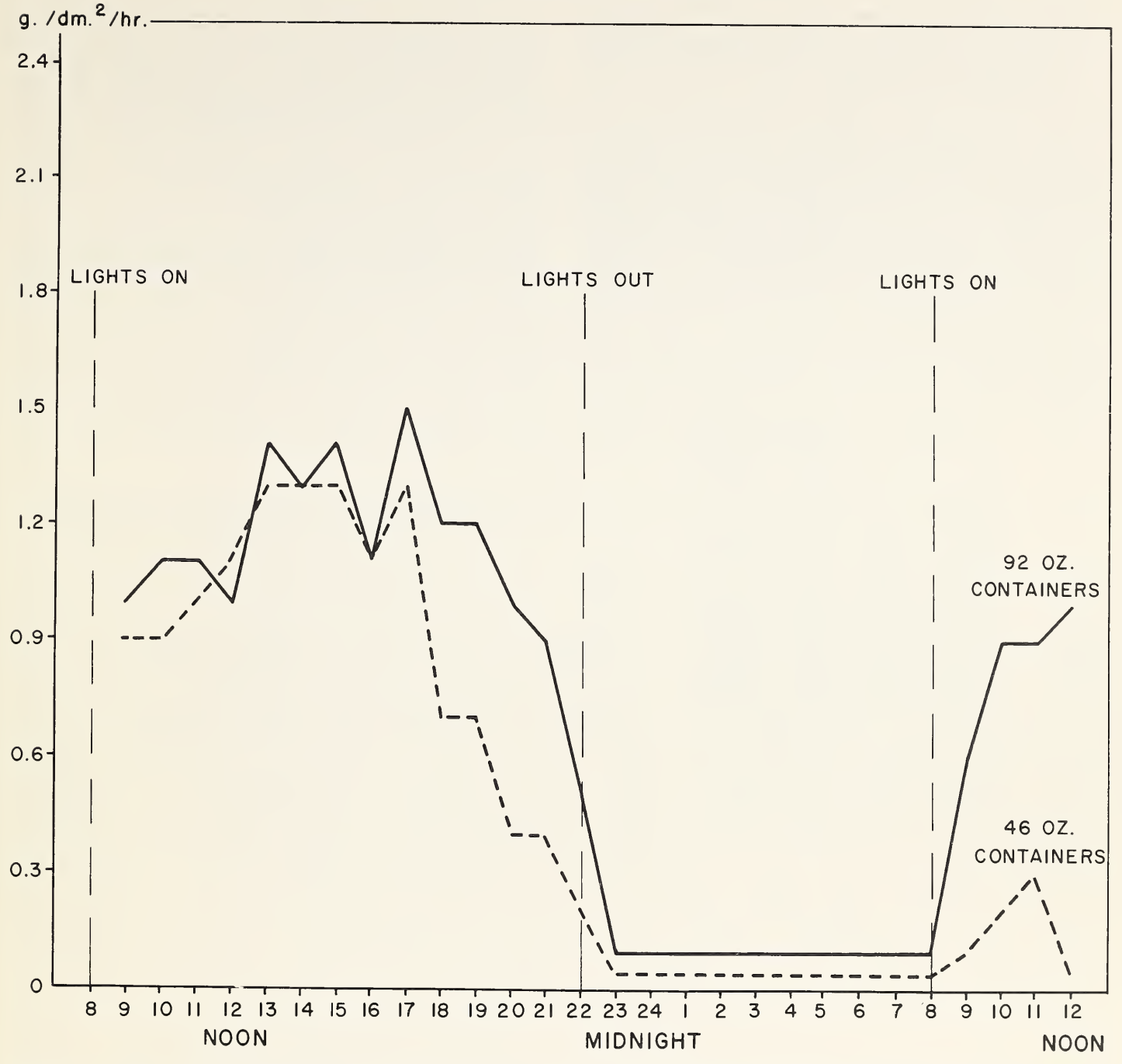


FIGURE 2.—Rate of transpiration of Red Kidney bean plants in different-sized containers when temperature was held at 25° C., relative humidity at 80 percent, and light at 0.82 cal. cm.$^{-2}$ min.$^{-1}$ for the entire 28-hour period.

their transpiration loss checked at a higher humidity (fig. 2) for a comparable period.

## Results and Discussion

In general, the transpirational pattern was not affected by the container size; however, the magnitude is different. The curves are highly significantly different from one another at either the high or low vapor pressure deficit (v.p.d.). At the termination of the experiment the final weight of plants in either size containers was not significantly different. This indicates the container size did not measurably affect plant growth.

Less water was lost at any given time-interval at the higher humidity (fig. 2), in contrast to that at the lower relative humidity (fig. 1). The fluctuations evidenced as blips in the transpirational curves are significant. Their cause is unknown but may be attributed to stomatal action. Only through careful monitoring of the stomatal condition can this point be resolved. Vaadia (*34*) has also shown a midday depression of transpiration in sunflower plants grown in Hoagland's solution—again the cause is unknown.

As a result of the findings in this experiment, the 46-ounce cans will continue to be used in studies of transpiration.

## TRANSPIRATION OF NUTRIENT-CULTURED VERSUS SOIL-GROWN PLANTS

For transpiration studies where soil moisture tensions are not considered to be an important parameter or where one wishes to avoid a gradual increase in soil moisture tension brought about by evaporation or transpiration, nutrient solution such as Hoagland's (*10*) is useful. At any one time-interval the liquid added to bring the solution up to a predetermined level is indicative of the water used by the plant in transpiration. An error may exist in the results if absorption by the roots does not parallel transpiration. Kramer (*14*) found that this is frequently the case.

A more precise method of determining the quantity of water transpired in a time-interval is by differences in weight of the container, plant, and solution at prescribed times.

Since an aerator system was necessary for satisfactory growth of Red Kidney bean plants in nutrient solution, the weight difference method

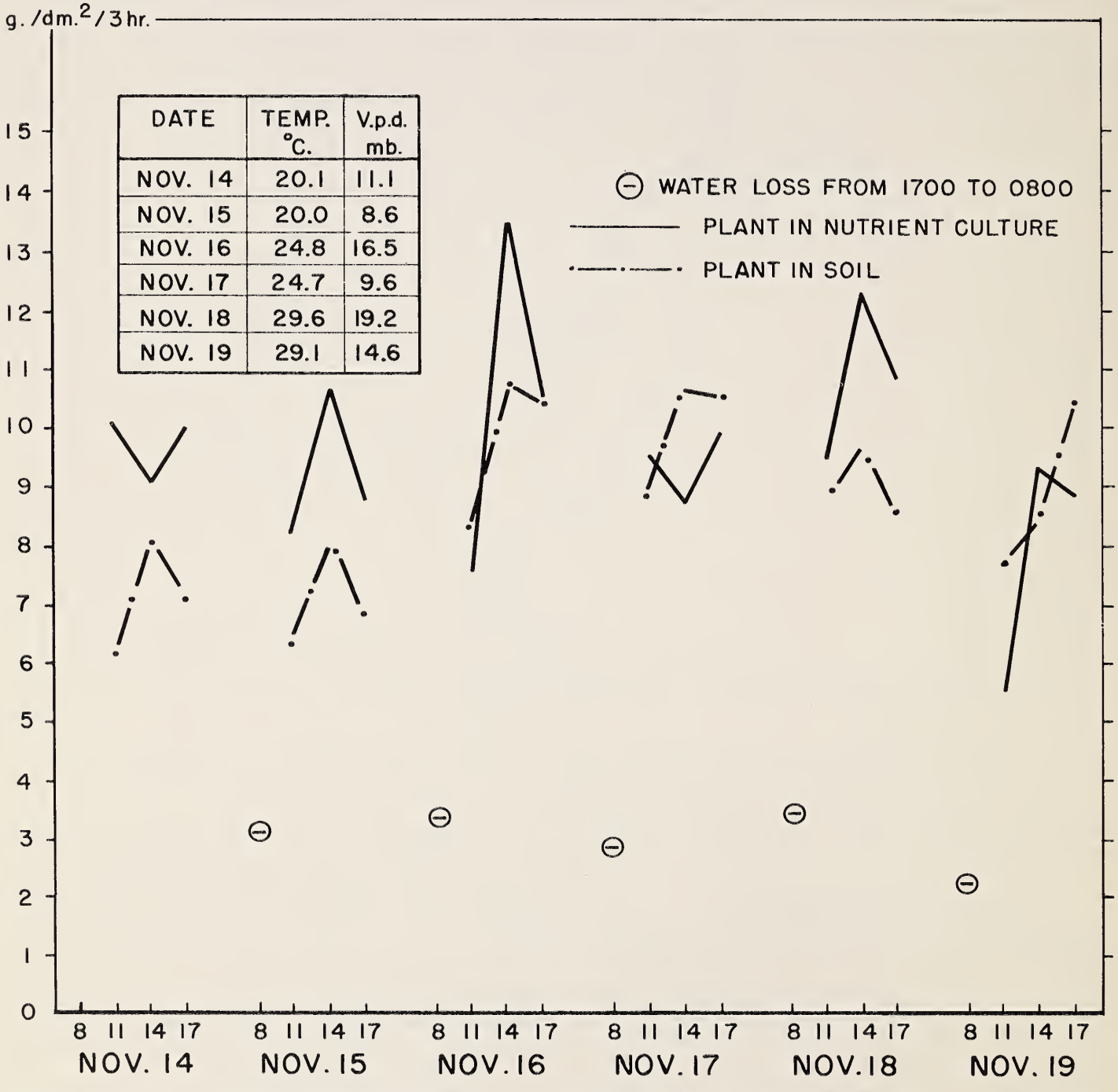


FIGURE 3.—Rate of transpiration of Red Kidney bean plants grown in soil or in nutrient solution. Sunlight equivalent for the group was 1.35 cal. cm.$^{-2}$ min.$^{-1}$

was found cumbersome; therefore, the method of determining the volume of liquid added was employed. This experiment permitted the comparison of transpiration by plants grown in nutrient culture with the transpiration by plants grown in soil (see next subsection, p. 7).

## Procedure

Red Kidney bean seeds were germinated and the plants grown until 3 weeks of age in growth chambers. They were grown in fertilized Cecil sandy loam. Growth conditions in small growth chambers up to the time of transfer to the growth room were 14 hours of light, temperature at 25° C., no control on relative humidity, but it ranged from 30 to 62 percent as measured by a hair hygrometer; and 10 hours of dark, temperature at 15° C., relative humidity of 94 to 97 percent. Light was obtained from a fluorescent-incandescent source giving approximately 2,000 ft.–c., or 0.70 cal. cm.$^{-2}$ min.$^{-1}$. Upon transfer of 60 selected plants to the growth room, the soil was washed from the roots of 24 representative plants. These plants were transferred directly into quart-size mason jars containing Hoagland's solution. The only change from Hoagland's formula (*10*) was that iron was supplied as iron chelate at 4.5 p.p.m. A transplanting shock was noted if the light intensity was initially high, but was overcome by conditioning of the plants at 0.35 cal. cm.$^{-2}$ min.$^{-1}$ for several days after transplanting. This method of starting plants was superior to any other and made it possible to use soil-and-nutrient-cultured plants in a comparable stage of growth. Water loss from the solution was measured at 3-hour intervals.

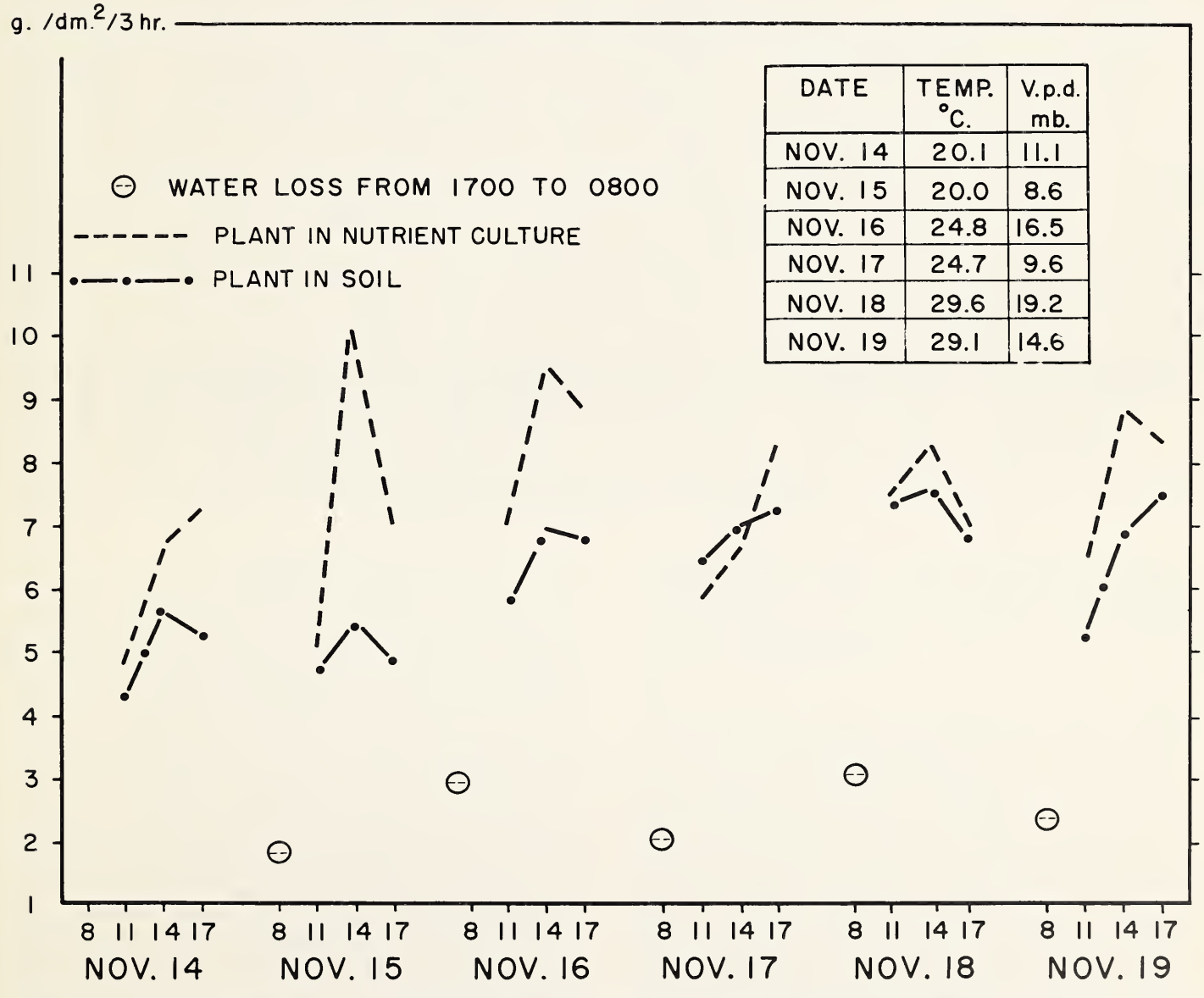


FIGURE 4.—Rate of transpiration of Red Kidney bean plants grown in soil or in nutrient solution. Sunlight equivalent for the group was 0.65 cal. cm.$^{-2}$ min.$^{-1}$

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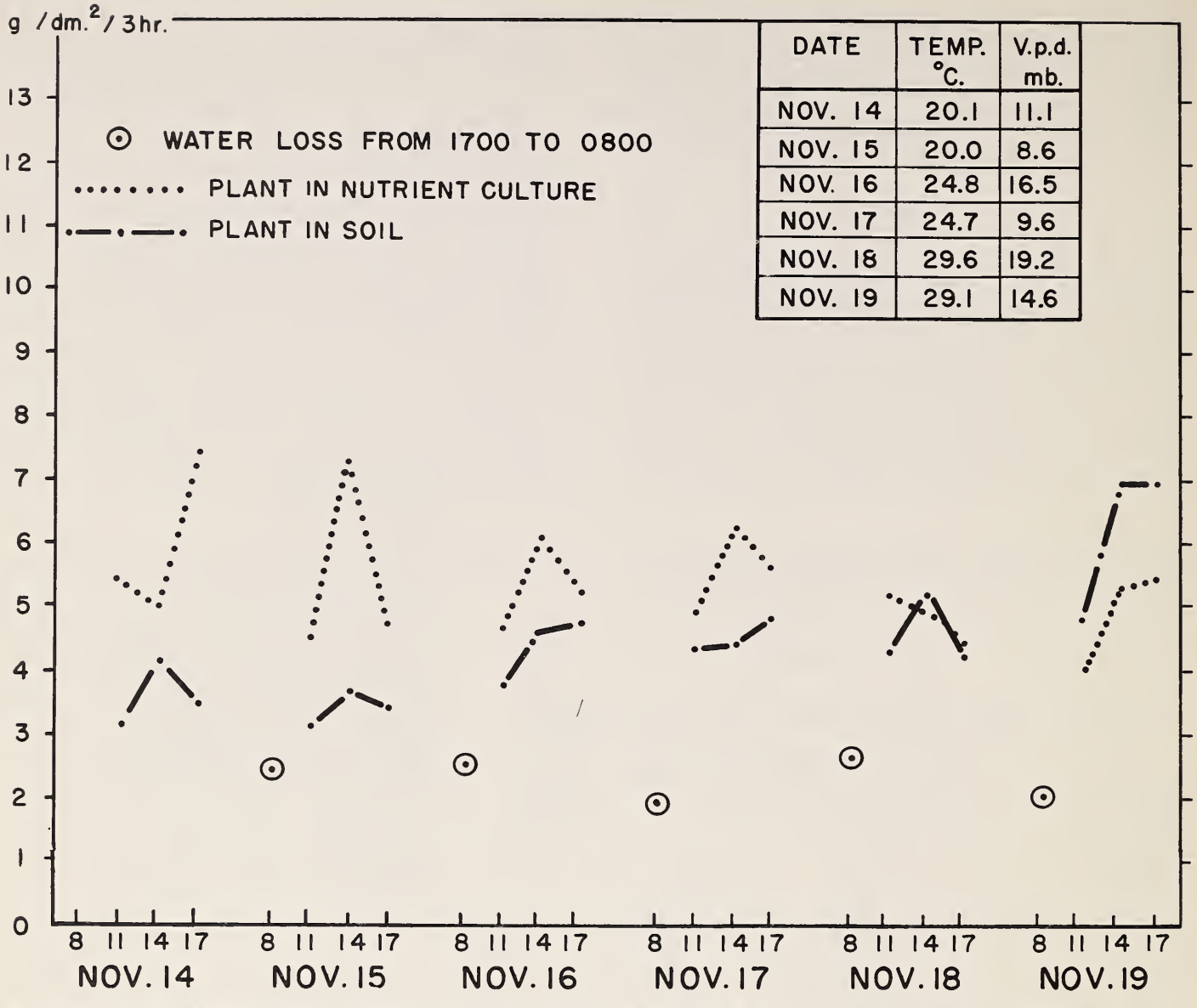


FIGURE 5.—Rate of transpiration of Red Kidney bean plants grown in soil or in nutrient solution. Sunlight equivalent for the group was 0.35 cal. cm.$^{-2}$ min.$^{-1}$

In figures 3, 4, 5, and 6, the 0800 reading is cumulative for water lost from 1700 the previous evening until 0800 the next morning. This reading was available only for the nutrient-cultured plants; no such data were available from the plants grown in soil, as their containers were placed in an inch of water for subirrigation at 1800 and removed for drainage at 2100.

During the preconditioning period plants in the growth room were grown under standard conditions of 25° C. and relative humidity of 50 percent. Once transpirational measurements were started on a population, any change in temperature or vapor pressure deficit (v.p.d.) from the standard conditions was of only 2 days' duration, after which growth room conditions were brought back to the standard for 2 days so that carryover effects of the treatment might be detected if they existed.

## Results

A definite trend of differences in transpiration of plants grown in the two media is obvious in figures 3, 4, and 5. The moisture lost from plants growing in nutrient culture was much greater than that in soil, especially at low temperatures and low light intensities. This is probably related to the availability of water for transpiration—all other factors having remained somewhat constant.

As light intensity increased (compare figs. 3, 4, and 5), an increase in transpiration occurred. The increase in transpiration is correlated with an increase in the ambient temperature of each bay, which increased with radiant energy. This rise in temperature increased the vapor pressure deficit and required correction as indicated in the next subsection.

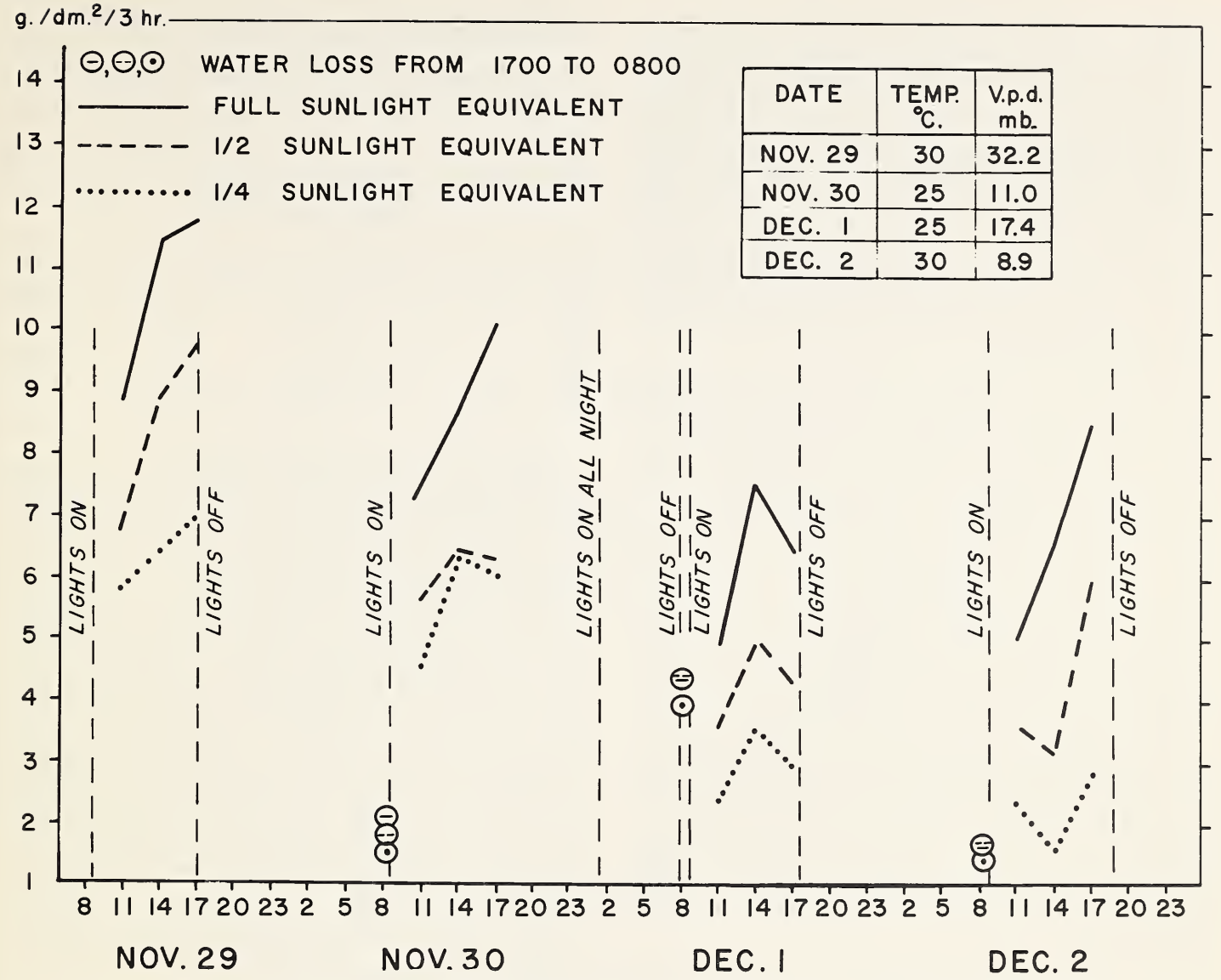


FIGURE 6.—Rate of transpiration of Red Kidney bean plants grown in nutrient solution at indicated temperatures, vapor pressure deficits, and radiant energy.

The data presented in this section are only indicative of trends; however, the general statement can be made that the transpiration rates of nutrient-cultured and soil-cultured plants are not always comparable. A reliable linear prediction equation has not yet been developed and appears to be more difficult to obtain for the nutrient-cultured plants than for the soil-grown plants.

Figure 6 indicates that a 24-hour light period causes a change in the transpirational ability of the plant. This is evidenced by the distinct drop in transpiration rate of plants on the day following the interrupted light period (December 1, fig. 6). It is also evident that the overnight consumption of water was higher during the all-night light period as compared to a normal dark night, probably because of an effect on the stomatal condition. The data were the result of a failure in circuitry, but because of their possible relevance to Vaadia's studies (*34*) they are included.

## EFFECTS OF ENVIRONMENTAL FACTORS ON TRANSPIRATION OF SOIL-GROWN RED KIDNEY BEAN PLANTS

A preliminary experiment was conducted in the high light-intensity growth chamber to test the control systems and to measure the effects of environment upon transpiration. Red Kidney beans were germinated in 46-ounce cans filled with Cecil sandy loam topsoil (2 kilograms air-dried). The beans were germinated and grown for 2 weeks in a constant environment growth box (see p. 5 for details) and then transferred to the growth chamber. The plants were preconditioned for 3 additional days under 0.65 cal. $cm.^{-2}$ $min.^{-1}$ radiant energy for 9 hours each day. Temperature and humidity were held constant at 25° C. and 50 percent relative humidity during the entire preconditioning period. The plants were

subirrigated each evening for 3 hours, starting at "lights out," and then drained until "lights on" the following morning. This procedure was followed from the beginning of the preconditioning period through the end of the experimental period.

Soil moisture tensions at the start of the day averaged 85±10 millibars (mb.) for all treatments. Tensions at the end of the data period each day ranged from an average of 172 mb. for the 0.35 cal. cm.$^{-2}$ min.$^{-1}$ light treatment to 457 mb. for the 1.35 cal. cm.$^{-2}$ min.$^{-1}$ treatment. Tensions at the end of the daily period averaged 216 mb. for the plants that received light intensities of 0.65 cal. cm.$^{-2}$ min.$^{-1}$.

Data were collected from five different plant populations for a total of 25 days during the experiments. Environmental conditions imposed were three light intensities, two vapor pressure deficits, and three ambient temperatures. The three light intensities were simultaneously imposed upon 10 plants for each energy level for all days of the experiment. The average intensities of each light level were 0.35 cal. cm.$^{-2}$ min.$^{-1}$, 0.65 cal. cm.$^{-2}$ min.$^{-1}$, and 1.35 cal. cm.$^{-2}$ min.$^{-1}$ for day lengths of 9 hours. Six combinations of the three temperatures and two vapor pressure deficits were programed during the experiments. Each combination was used for a unit time period of 1 day.

Table 1 lists the six temperature-vapor pressure deficit combinations and the number of days that each combination was programed. Variations from the programed conditions occurred on several days owing to inadequate control. Actual conditions obtained were used and, therefore, variations that did occur are accounted for in the analysis. The table also indicates the relative humidity for each combination.

Data collected during the experiment included transpiration, radiant energy, wet and dry bulb temperatures, and leaf area.

Transpiration was considered to be equal to the loss in total weight of the plant, soil, and container for the period under consideration. Period length ranged from 1 hour to 1 day. Soil moisture tension was estimated from the weight of the plant, soil, and container.

Radiant energy was continuously monitored and recorded under each light treatment by Beckman-Whitley total radiometers.[2] During the experiment the transducer temperature of the radiometer exceeded ambient temperature owing to increased radiant energy. The increases were 0° C. for 0.35 cal. cm.$^{-2}$ min.$^{-1}$, 2° for 0.65 cal. cm.$^{-2}$ min.$^{-1}$, and 5° for 1.35 cal. cm.$^{-2}$ min.$^{-1}$. Leaf temperatures of top leaves were almost identical to the transducer temperatures, and therefore the values given were used in calculating adjusted temperatures and vapor pressure deficits of the plant leaves under the three radiation levels.

[2] The use of this or other patented equipment in this study does not imply approval of the product to the exclusion of others that may also be suitable.

TABLE 1.—*Temperature and vapor pressure deficit combinations programed for effects of environmental factors on transpiration of soil-grown Red Kidney bean plants, Watkinsville, Ga., 1961*

| Temperature (°C.) | Vapor pressure deficit | Relative humidity | Days |
|---|---|---|---|
| | *Mb.* | *Percent* | |
| 20 | 3. 2 | 86 | 3 |
| 20 | 15. 8 | 32 | 2 |
| 25 | 3. 2 | 90 | 3 |
| 25 | 15. 8 | 50 | 11 |
| 30 | 3. 2 | 92 | 2 |
| 30 | 15. 8 | 63 | 4 |

Wet- and dry-bulb temperatures were measured and recorded in the exhaust stream from the chamber. The relative humidity of the exhaust air was determined from psychrometric tables, and vapor pressure deficits were calculated by a computer program. The vapor pressure deficit was considered to be equal to the vapor pressure of water at the leaf temperature minus the vapor pressure of water in the exhaust stream. Leaf temperature was estimated as being equal to the dry-bulb temperature plus the radiation adjustment factor of 0°, 2°, or 5° C.

Leaf area was estimated each day for each plant. The estimate was made by accumulating the estimated leaf area for each leaf. Estimates were made with sample templates, and reproducibility was about ± 5 percent.

Time was recorded as minutes after midnight for convenience of processing the data through a computer unpacking program.

The data collected were analyzed by a multiple linear regression analysis[3] using IBM program 06.2.002.8[4] for the 650 computer. Regression equations were determined and are listed below. Simple correlation coefficients were run by IBM program 06.2.006.1[5] for the 650 computer.

Regression equation 1 for transpiration per plant for a 9-hour day was obtained from all the data collected during the 25 days of the experiment. The total transpiration for each plant for each day was used in this analysis rather than breaking transpiration down into periods within the days. The equation is as follows:

$$E_d = -6.34 + 0.0141\,R_dL + 0.496\,V_aL + 1.101\,A \quad (1)$$

where $E_d$ = transpiration expressed in grams of water per plant per day (plant$^{-1}$ day$^{-1}$);

[3] HARVEY, W. R. LEAST SQUARE ANALYSIS OF DATA WITH UNEQUAL SUBCLASS NUMBERS. U.S. Dept. Agr. ARS 20–8, 157 pp. 1960.

[4] IBM Library File 06.2.002.8. Data unpacking and transformation; multiple regression format.

[5] IBM Library File 06.2.006.1.

$R_d$ = total radiant energy expressed in calories per square centimeter per day (cal. cm.$^{-2}$ da.$^{-1}$) ;

$L$ = leaf area of plant expressed in square decimeters per plant (dm.$^2$ plant$^{-1}$) ;

$V_a$ = adjusted vapor pressure deficit of the top leaves of the plant expressed in millibars (mb.) ;

$A$ = age of the plant in days.

Figure 7 shows the agreement between actual transpiration and that accounted for by the parameters of regression equation 1. This equation accounts for about 86 percent of the variability in transpiration that occurred during the 25 days of the experiment. Each point is an average of 10 plants.

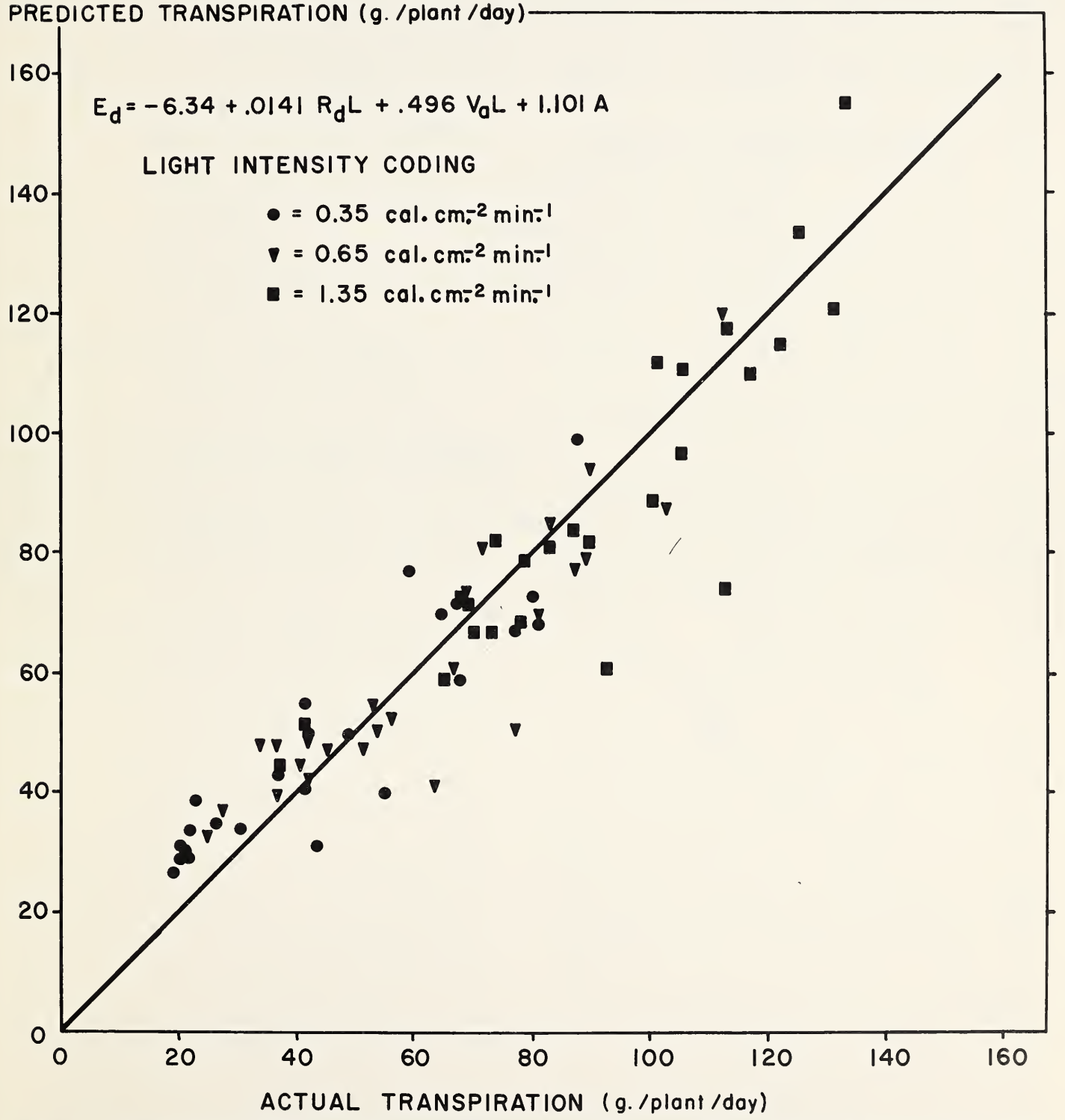


FIGURE 7.—Relationship between actual measured transpiration per plant per 9-hour day for 25 days and predicted transpiration as calculated by regression equation 1. Each point is the average of 10 plants.

The data from 9 "standard days" were analyzed separately, and equation 2 is an expression that accounts for 88 percent of the variability in transpiration under essentially constant conditions.

$$E_d = 17.26 + 0.0531\ R_dL + 0.157\ V_aL \qquad (2)$$

Radiant energy and leaf area account for the major differences in transpiration from plants subjected to constant temperature and vapor pressure deficits. Figure 8 illustrates the relationship between actual measured daily transpiration and the estimated daily transpiration calculated by regression equation 2 of this section. Each point is an average of 10 plants.

The data for transpiration by periods within a day were also analyzed for 17 days. All days were approximately 9 hours in length, but the number of equal-length periods within a day ranged

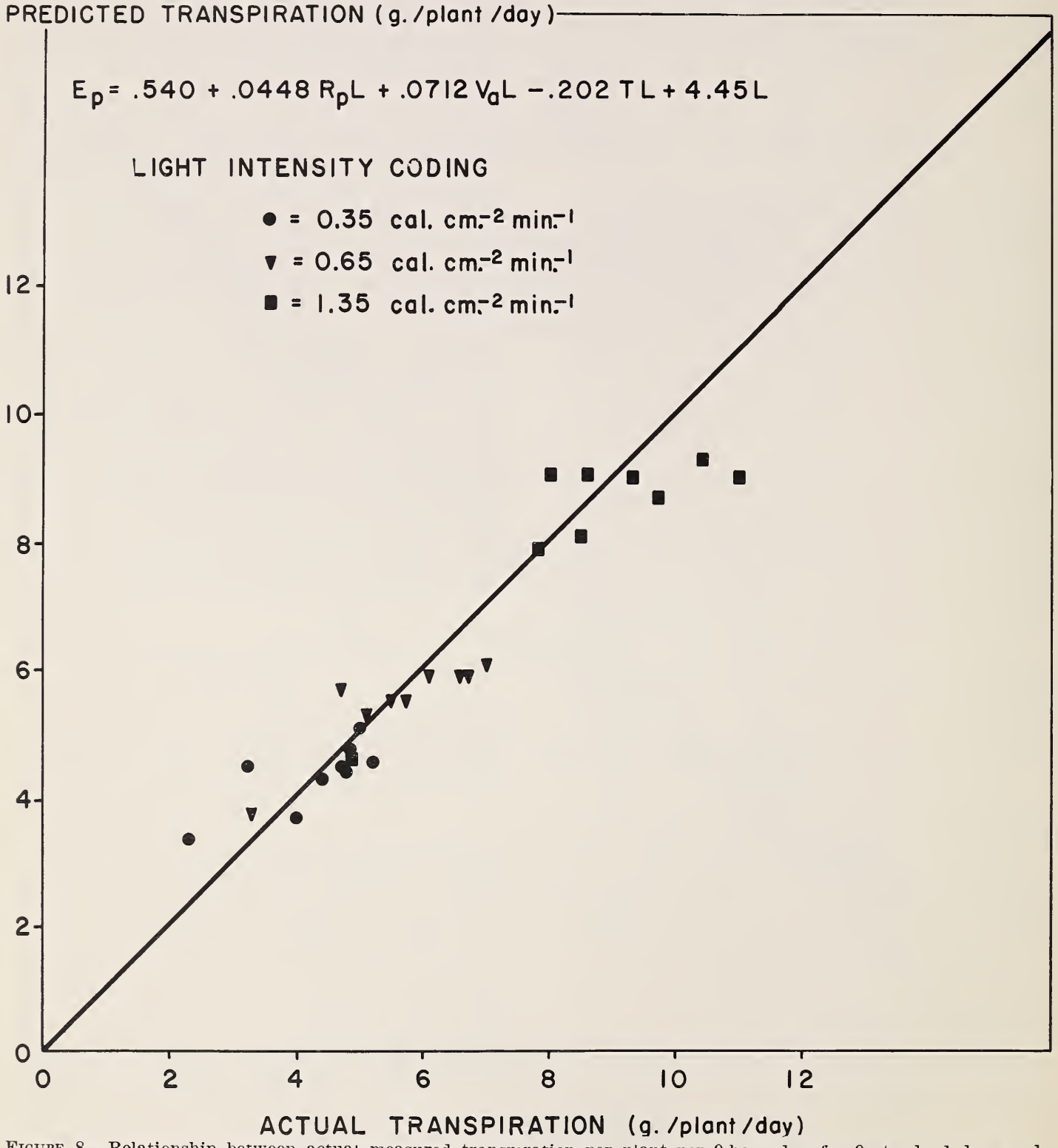


FIGURE 8.—Relationship between actual measured transpiration per plant per 9-hour day for 9 standard days and predicted transpiration as calculated by regression equation 2. Each point is an average of 10 plants.

from 4 to 9 hours. The data available were as follows:

| *Periods measured* | *Days data obtained Number* |
|---|---|
| 4 | 3 |
| 5 | 3 |
| 8 | 1 |
| 9 | 10 |
| Total | 17 |

Regression equation 3 was developed from these data.

$$E_n = 8.32 + 0.00275R_nL + 0.0986V_aL + 0.146t_n + 0.00294\Sigma t_{n-1} - 0.108L \quad (3)$$

where $E_n$ = transpiration expressed in grams of water per plant per period.

$R_n$ = total radiant energy expressed in calories per square centimeter per period (cal. cm.$^{-2}$ period$^{-1}$).

$L$ = leaf area of plant expressed in square decimeters per plant (dm.$^2$ plant$^{-1}$).

$V_a$ = adjusted vapor pressure deficit of the top leaves of the plant expressed in millibars.

$t_n$ = duration of period in minutes.

$\Sigma t_{n-1}$ = duration of period of time from "lights on" to start of period "$n$" expressed in minutes.

Figures 9, 10, and 11 illustrate the relationship between actual measured transpiration and estimated transpiration as calculated by regression equation 3. This equation accounts for about 81 percent of the variability in the transpiration. This relatively poor relationship is probably caused by the importance of period length in the analysis.

The analysis would have been more meaningful if $R_nL$ and $E_n$ had been converted to a unit-of-time basis. The significance of the positive slope of the constant for $\Sigma t_{n-1}$ is subject to speculation. It is in complete agreement with the results on sorghum (p. 16) and is probably related to low soil moisture tensions and restricted aeration.

The negative slope of the leaf area constants could be a manifestation of the effect of self-shading of bean plants, which increases with size.

The parameters $R_dL$, $R_nL$, and $V_aL$ were not used without justification. It was recognized that plant size was a dominant factor in transpiration and should be held constant. The possibility of holding plant size constant by multiplying the various environmental parameters by leaf area was investigated. Table 2 presents the results of this study. All values represent the simple correlation coefficient between transpiration and the product of the environmental factor times leaf area. The code series, 5X00, represents data from the 9 standard days used for regression equation 2. During these days environmental conditions remained constant; however, leaf area varied 100 percent. The code series, 6X02, represents data for 9 periods within day "322," which was one of the 9 standard days.

TABLE 2.—*Simple correlations between actual transpiration and environmental parameters*

| Variables | Light intensity [1] | | | |
|---|---|---|---|---|
| | All pooled | 0.35 cal. cm.$^{-2}$ min.$^{-1}$ | 0.65 cal. cm.$^{-2}$ min.$^{-1}$ | 1.35 cal. cm.$^{-2}$ min.$^{-1}$ |
| | *5000* | *5100* | *5200* | *5400* |
| $R_d$ vs. $E_d$ | 0.628 | 0.436 | 0.171 | 0.254 |
| $R_dL$ vs. $E_d$ | .911 | .891 | .888 | .910 |
| | *6002* | *6102* | *6202* | *6402* |
| $R_n$ vs. $E_n$ | 0.734 | 0.450 | 0.447 | 0.465 |
| $R_nL$ vs. $E_n$ | .913 | .904 | .848 | .881 |
| | *5000* | *5100* | *5200* | *5400* |
| $V_a$ vs. $E_d$ | 0.580 | 0.084 | 0.010 | 0.069 |
| $VL$ vs. $E_d$ | .613 | .791 | .897 | .866 |
| $V_aL$ vs. $E_d$ | .885 | .791 | .902 | .880 |
| | *6002* | *6102* | *6202* | *6402* |
| $V_a$ vs. $E_n$ | 0.527 | 0.171 | 0.070 | 0.017 |
| $V_aL$ vs. $E_n$ | .741 | .778 | .578 | .611 |
| | *3000* | *3100* | *3200* | *3400* |
| $V$ vs. $E_d$ | 0.416 | 0.665 | 0.522 | 0.385 |
| $V_a$ vs. $E_d$ | .708 | .665 | .558 | .474 |
| $VL$ vs. $E_d$ | .639 | .886 | .870 | .770 |
| $V_aL$ vs. $E_d$ | .879 | .886 | .893 | .846 |

[1] Italic 4-digit numbers are codes assigned to analyses referred to in this experiment.

The code series 3X00 represents data for the 25 days used for regression equation 1. For all three code series, values of $X$ represent the following light-intensity treatments.

| $X$ | *Light-intensity treatment* |
|---|---|
| 0 | All intensities pooled. |
| 1 | 0.35 cal. cm.$^{-2}$ min.$^{-1}$ only. |
| 2 | 0.65 cal. cm.$^{-2}$ min.$^{-1}$ only. |
| 4 | 1.35 cal. cm.$^{-2}$ min.$^{-1}$ only. |

The data in table 2 clearly indicate that total radiant energy ($R_d$ or $R_n$) times leaf area ($L$) and vapor pressure deficit ($V$ or $V_a$) times leaf area ($L$) are more closely correlated with transpiration than the simple environmental factors radiant energy ($R_d$ or $R_n$) and vapor pressure deficit ($V$ or $V_a$). The table also indicates a slightly better correlation between adjusted vapor pressure deficits and transpiration than between unadjusted vapor pressure deficits and transpiration.

The linear analysis used for this experiment has been useful but is limited in its capability, because some relationships are nonlinear. In future analyses mathematical models must be tested and modified if necessary. Nonlinear response estimates for the different environmental parameters based upon theory must be inserted in place of the rather simple mathematical model

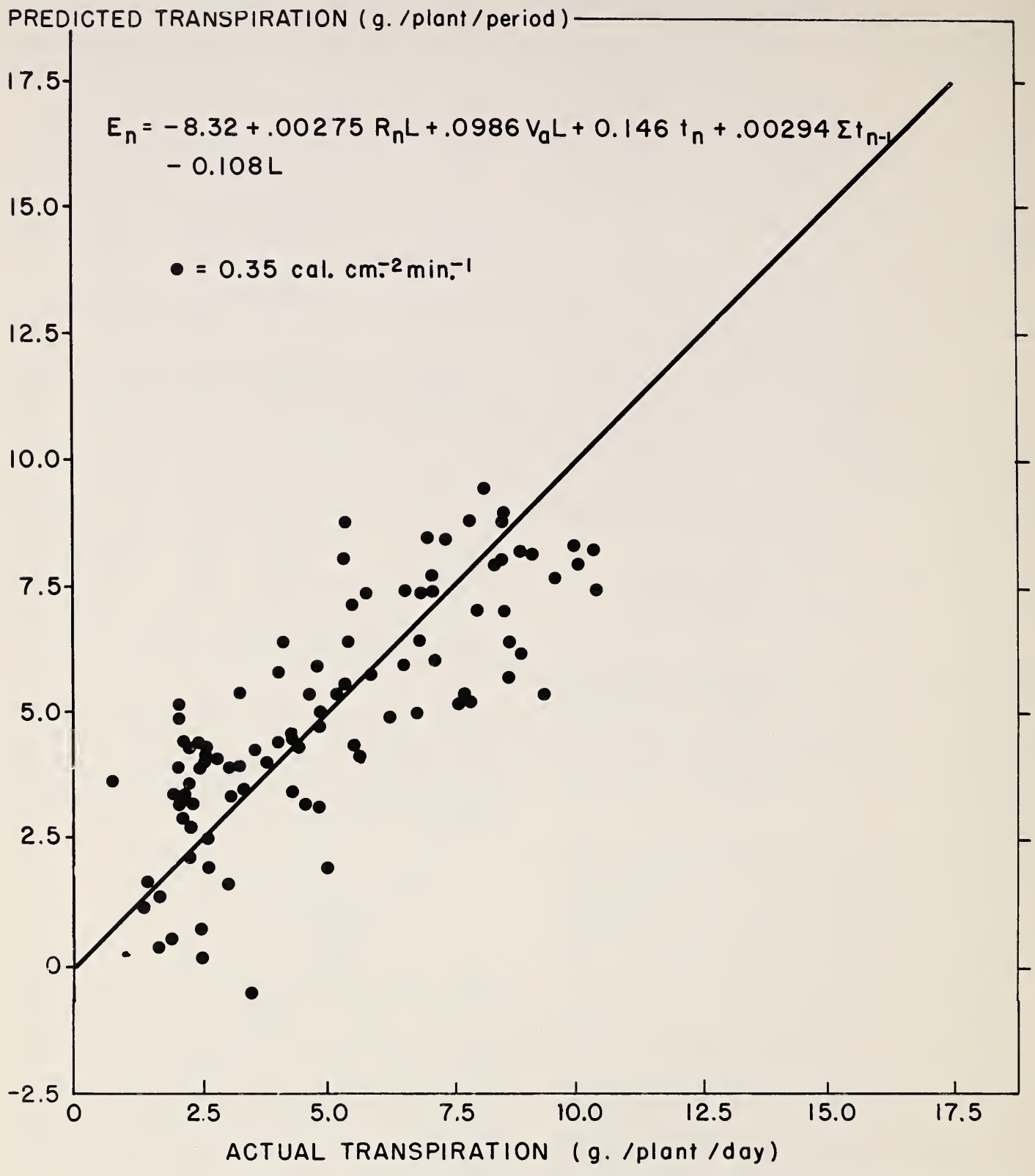


FIGURE 9.—Relationship between actual measured transpiration per plant per period for 17 days and predicted transpiration as calculated by regression equation 3. Each point is the average of 10 plants subjected to a radiant energy level of 0.35 cal. cm.$^{-2}$ min.$^{-1}$

used for the analysis reported here. Computer facilities are available and the additional programs necessary to attempt the proposed refinements in analysis will be written.

## Summary

It has been established that the high light-intensity growth chamber is capable of controlling radiant energy, ambient temperature, and vapor pressure deficit within the limits required to conduct quantitative transpiration experiments. The high light-intensity capabilities of the chamber permit the design of controlled experiments which were previously not possible.

The data indicate that the consideration of purely physical parameters accounted for less than 90 percent of the variability in transpiration. The remaining variability must be interpreted as biological.

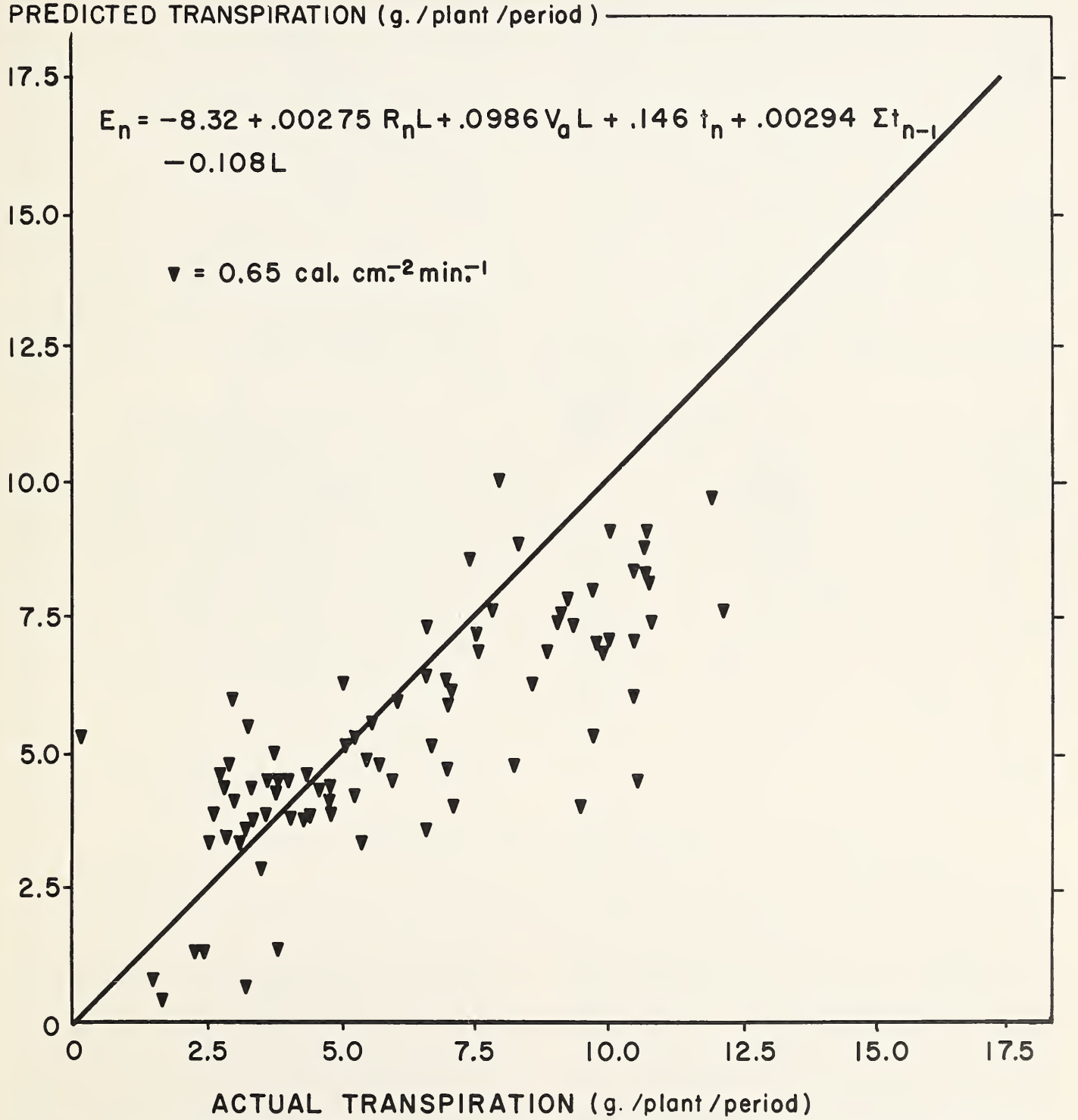


FIGURE 10.—Relationship between actual measured transpiration per plant per period for 17 days and predicted transpiration as calculated by regression equation 3. Each point is the average of 10 plants subjected to a radiant energy level of 0.65 cal. cm.$^{-2}$ min.$^{-1}$

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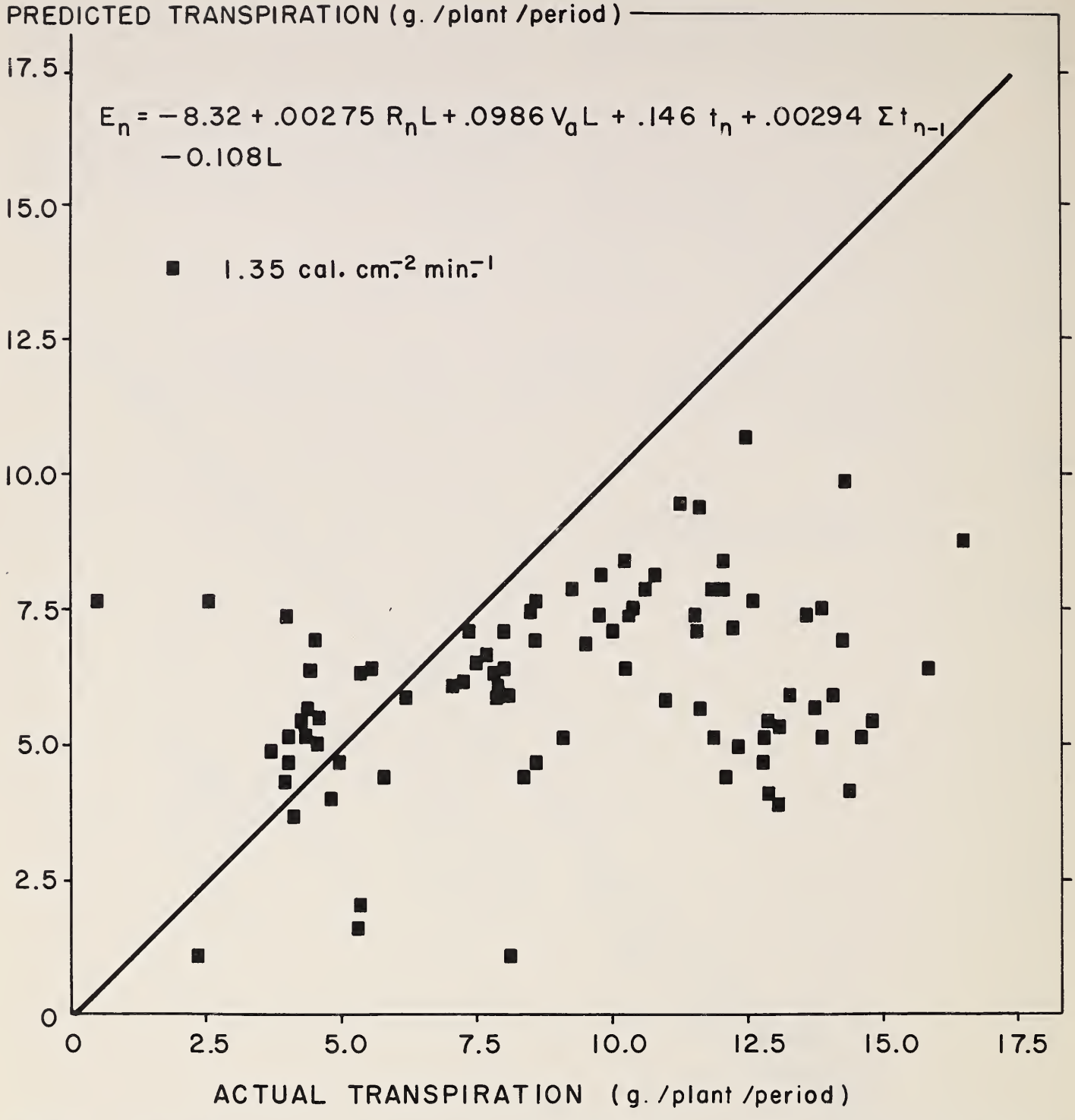


FIGURE 11.—Relationship between actual measured transpiration per plant per period for 17 days and predicted transpiration as calculated by regression equation 3. Each point is the average of 10 plants subjected to a radiant energy level of 1.35 cal. cm.$^{-2}$ min.$^{-1}$

The experiment reported here provided data that, although not reported, indicate that previous environmental conditions affect transpiration and plant growth. The data suggest the possibility that high vapor pressure deficits during the preceding light period can retard leaf enlargement and reduce transpiration on the following day. The data also indicate that long dark periods may increase transpiration rates during the following light period.

Temperature appears to have an indirect positive effect upon transpiration to the extent that it increases the vapor pressure deficit. However, the direct effect of temperature upon transpiration appears to be negative for values above 30° C. Since the experiment was not designed to collect information about these parameters, the data are inadequate to support definite statements. Trends are indicated, however, and studies of this nature are desired for refinement of regression equations.

# EFFECT OF SOIL MOISTURE TENSIONS ON TRANSPIRATION OF TWO STRAINS OF GRAIN SORGHUM AND A GRAIN SORGHUM-SUDANGRASS CROSS

Interest in the use of water by plants has increased rapidly since 1950, and there has been much controversy as to the effect of soil moisture tension on transpiration of plants. Veihmeyer and coworkers [6] concluded that ". . . transpiration was not affected by variations of soil moisture within the range from field capacity to permanent wilting percentage." On the other hand, work by Letey and Blank (*17*) shows that transpiration diminishes as soil moisture tension increases. Rijtema (*23*) states that reduction of transpiration is dependent upon conditions of the atmosphere, root distribution, soil moisture suction, and capillary conductivity of the soil.

This section deals with a part of a study concerned with the influence of light, relative humidity, and soil moisture tension on transpiration by sorghum plants. It is somewhat incomplete in that the data have not received full statistical treatment.

## Experimental Procedure

Seeds of two strains of grain sorghum *Sorghum vulgare* (Martin and Combine Kafir 60) and a grain sorghum-sudangrass cross (DeKalb SX–11) were germinated in vermiculite in a germination chamber at 30° C. and 95 percent relative humidity. After 44 hours of germination time, the sprouted seed were transplanted into 46-ounce fruit juice cans, three seedlings being planted in each can. A much larger population of plants was prepared than was needed so that the more uniform plants could be selected for the study. Each can contained 1,386 grams (on an oven-dry basis) of Cecil sandy clay loam (0- to 6-inch depth) into which was thoroughly mixed a 4–12–12 fertilizer at the rate of 3,000 pounds per acre. The cans were equipped with porous gypsum plates and a copper outlet tube, so that after each irrigation a vacuum could be applied for positive drainage of excess water from each can.

The cans containing the seedlings were placed in the controlled environment growth room under full-light intensity [7] at 25° C. and 60 percent relative humidity. Five days later it was necessary to move the plants to a greenhouse because of the failure of the growth room compressor. At 11 days of age the plants were thinned to one plant per can, leaving the most vigorous plant in each can. A sheet of white polyethylene plastic was placed around each plant and over the top of the can to prevent evaporation of moisture from the soil surface. This plastic sheet was taped in place with masking tape, and a trap door that could be taped shut was cut in the plastic so each can could be irrigated from the top.

When the plants were 14 days old, 15 of the most uniform plants of each strain were moved back to the growth room where they were kept at full light intensity, 25° C. and 60 percent relative humidity for four 12-hour days. The experiment was set up in a randomized complete block design in three replications, one replication being under each of the three light bays in the growth room.

The overall experiment consisted of two parts: Experiment A—a study of the effect of light intensity and relative humidity on the transpiration of three sorghum strains; and experiment B—a study of the effect of soil moisture tension on transpiration of three sorghum strains.

When the plants were 18 days old, experiment A was begun and followed the schedule given below for 13 days.

| Day of week | Light intensity | Relative humidity |
|---|---|---|
| | | *Percent* |
| Monday | One-half | 60 |
| Tuesday | Full | 90 |
| Wednesday | Full | 60 |
| Thursday | Full | 30 |
| Friday | One-half | 90 |
| Saturday | One-half | 30 |
| Sunday | Full | 60 |
| Monday | Full | 30 |
| Tuesday | One-half | 90 |
| Wednesday | Full | 90 |
| Thursday | One-half | 60 |
| Friday | Full | 60 |
| Saturday | One-half | 30 |

Experiment A will not be discussed further at this time, as the data from this part of the overall experiment have not been fully analyzed.

When the plants were 31 days old, they were irrigated and drained in preparation for experiment B. As there were some nitrogen and potassium deficiencies showing up on the plants, a complete nutrient solution was added to this irrigation water. The controlled environment growth room was kept at 25° C. and 60 percent relative humidity at full light intensity for 12-hour days and at 20° and 80 percent relative humidity for 12-hour nights. The plants were kept at these conditions until they permanently wilted. Transpirational water loss was determined by weighing each can at 2-hour intervals during the daylight period from 0700 to 1900.

[6] Veihmeyer, J. J., Pruitt, W. O., and McMillan, W. D. soil moisture as a factor in evapotranspiration equations. Amer. Soc. Agr. Engin. Ann. Meeting, Paper 60–202, 1960. (Copy may be obtained from American Society of Chemical Engineers, P.O. Box 2229, St. Joseph, Mich.)

[7] Full light intensity in this study is radiation equal to 1.35 cal. $cm.^{-2}$ $min.^{-1}$. One-half light intensity is 0.65 cal. $cm.^{-2}$ $min.^{-1}$

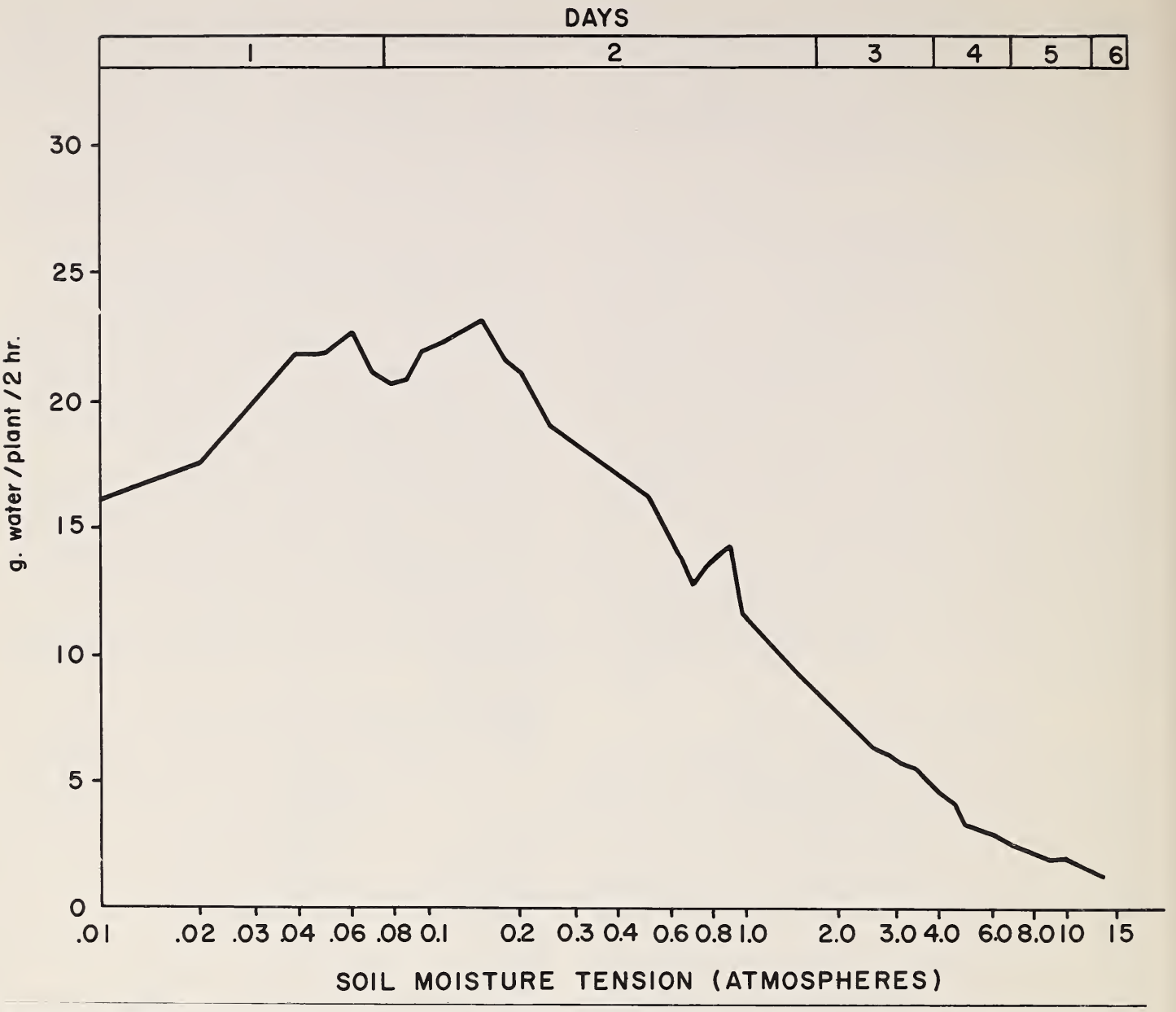


FIGURE 12.—Effect of soil moisture tension on the combined transpiration rate of two strains of grain sorghum and a grain sorghum-sudangrass cross.

As each plant permanently wilted, it was removed from the growth room, the aboveground part was removed, and the can of soil weighed. The soil moisture tension in the can of soil at permanent wilting was assumed to be 15 atmospheres. Thus, by adding the periodic transpirational losses of water back to the final can weight and relating this to a moisture desorption curve for the soil used in the study, it was possible to determine the transpiration rate of a plant at a given soil moisture tension.

## Results and Discussion

Figure 12 shows a composite curve that resulted from plotting average water loss per plant in grams per 2-hour period against soil moisture tension in atmospheres for three strains of sorghum. The scale across the top of the graph indicates the average time in days that was required for the plants to lower the soil moisture content enough to result in the soil moisture tensions shown on the bottom axis.

The overall curve shows how closely transpiration is related to soil moisture tension. Of particular interest is the break in the curve that occurred between 0.15- and 0.2-atmosphere tension and the subsequent downward trend in rate of transpiration with increasing soil moisture tensions.

An examination of the curves in figure 13, where each strain is plotted separately, shows that this break in the curve may vary with the rate of water removal from the soil by the plant. The break occurred near 0.1-atmosphere tension for DeKalb SX–11, the high-transpiring strain; however, it was in the neighborhood of 0.2-atmosphere ten-

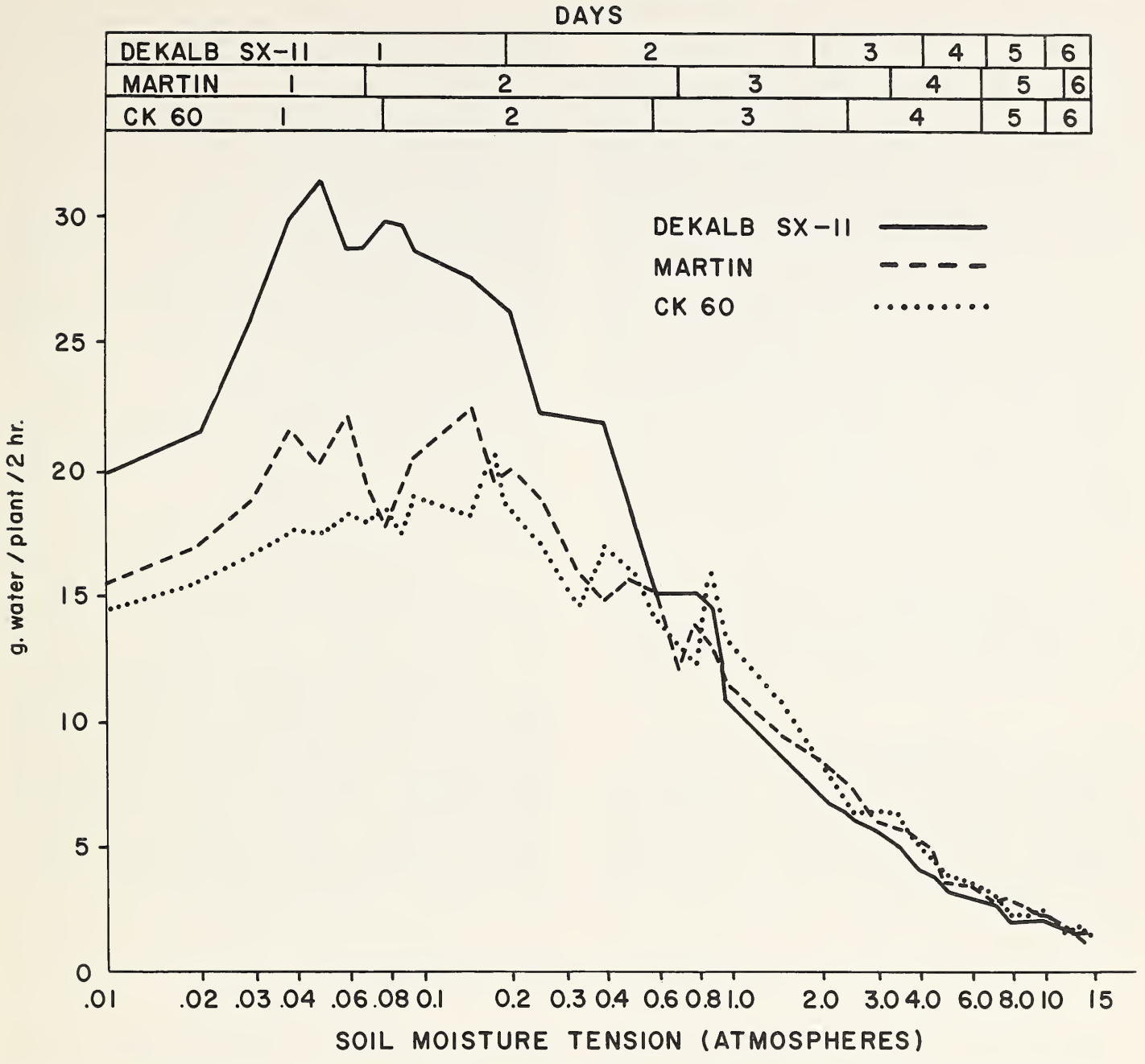


FIGURE 13.—Effect of soil moisture tension on transpiration by two grain sorghums and a grain sorghum-sudangrass cross.

sion that the break occurred for the two lower water-using strains. These breaks indicate the point at which the soil could no longer supply water to the plant roots at the rate water was being transpired by the plant. Changes in soil temperature, soil composition, soil compaction, and other physical properties may shift this breaking point on the curve. This would only be true if the aforementioned physical factors affect the movement of soil moisture other than by their effect on soil moisture tension.

The irregularities in the curve (fig. 12) that occurred at approximately 0.08- and 0.7-atmosphere tensions can be explained by two factors: (1) At high soil moisture contents, sorghum plants growing in 46-ounce cans build up to a peak transpiration rate during each day; (2) at nighttime when there is little removal of soil moisture by the plant, some soil moisture moves into the soil from which the plant root has removed moisture during the previous day.

The curves in figure 13 show that the dips in the curve at 0.08- and 0.7-atmosphere tensions were at the ends of the first and second days, respectively, for two of the three strains. The dips during the first day on the curves for SX–11 and Martin were reductions in transpiration that also have been observed with plants other than sorghum, and were possibly caused by midday closing of stomata, or by soil moisture conduction rates

that were lower than the transpiration rates of the plants.

The peaks before and after the first dip and the peak after the second dip in figure 12 are the result of daily buildup in transpiration rates by the different strains. The first peak is due to the composite effect of all three strains, and the second and third peaks are the combined effect of Martin and CK 60. After the first day SX–11 no longer exhibited a peak in daily transpiration. This phenomenon was probably caused by the removal of soil moisture by this high-transpiring strain at rates greater than the rates of soil moisture conduction into the soil in contact with roots. Martin and CK 60, the low water users, exhibited a daily transpiration peak into the fourth day. It is suggested that these phenomena are related in some respects to the unsaturated flow of soil moisture and, indeed, tempt one to speculate as to the possible use of well-distributed fibrous root systems in studies of the unsaturated flow of soil moisture.

Another point of interest is that poor aeration of the soil at high moisture contents apparently had a depressing effect on transpiration. Figure 13 shows that, for all three strains, the initial rate of transpiration the first day is lower than the initial rate on the second day.

## FUTURE STUDIES

Many aspects of environmental effects on transpiration remain to be studied. Data under controlled environment as outlined in this report are available on only two species. Approximately 250,000 species of plants cover the face of the earth, and it is therefore necessary to study many more representative species before universally reliable prediction equations can be found.

All phases of the micrometeorology around the plant need to be measured precisely so that their effects can be determined. For instance, future experiments should be designed to eliminate plant shading as a variable. Two approaches are possible. The first approach is to work with a closely clipped grass that would permit accurate calculations of the intercepted radiant energy, which is the most important single parameter in the transpiration potential. A second approach would be to design experiments to determine self-shading factors for the different plants. Light-quality effect on transpiration remains to be measured.

In addition to reducing or eliminating the shading variable, experiments should be designed to determine the effect of soil moisture tension upon transpiration. Data reported in the preceding subsection (p. 15) indicate that soil moisture tension can be a limiting factor in transpiration. The problem is primarily one of hydraulic conductivity, unsaturated flow, and moisture transfer. Also the effect of soil fertility on transpiration remains to be studied thoroughly across a root and soil-water interface.

A time-lapse photographic record will aid in evaluating stomatal control on transpiration, although complete automation appears impossible.

In data reported on pages 7 to 14, radiant energy appears to be the most influential factor on transpiration. Its effect on stomatal behavior, heat exchange of the plant and its environment, and water use economy is unknown. A study is being initiated to define radiant energy effect on the transpiration of corn plants.

# GUARD CELL ACTION

As outlined in the report published October 1961 (*35*), the mechanism of operation of guard cells appears to be intimately associated with a light effect. However, the light effect must be reconciled with the diversities found in guard cell action. Loftfield (*18*) places plants in three groups, according to their stomatal behavior throughout a 24-hour period. The first group is composed of the cereals in which night opening does not occur under favorable or unfavorable conditions. Group two includes most of the thin-leaved mesophytes. Under optimum conditions the stomata of the mesophytes are open in the day and closed at night. They may close at midday and open at night under unfavorable conditions. In the third group the stomata of plants are open to a greater or lesser degree throughout the day and the night, although severe water deficit causes closure in the daytime. All the above groups are probably affected to some extent by water deficits. This effect has been termed by Stålfelt (*31*) as a hydroactive one.

In most cases stomatal openings have been found to decrease upon subjection of the plant to a water deficit. The deficit may originate from vapor pressure deficits of the air or increased soil moisture tension, or both, and is reflected in the water balance of the plant. It is difficult at times to delineate hydroactive effects from what are called passive movements. Passive opening movements are caused by a water deficit in the epidermal cells while pressure still exists in the guard cells, causing an open stoma. Passive closing movements may be brought about by satisfying the aforementioned deficit in the epidermal cells, which forces the stoma shut by pressure on the guard cells. Photoactive, hydroactive, and the passive systems are all operable in guard cell action and must be considered individually and collectively when attempting to correlate transpira-

tion with the microclimate. Several approaches to understand these systems have been used and are listed under such sections.

## GUARD CELLS OF ALBINO CORN

An absence of guard cell starch in albino corn was reported (*35*). The finding was contrary to that of Shaw (*28*), who found starch in the guard cells of albino barley, and Sayre (*26*), who reported it in albino corn. Leitgeb (*16*) had earlier reported the presence of starch in stomata devoid of chlorophyll. Using a large population of albinos, a check for guard cell starch by means of iodine-potassium-iodide showed it was present in the guard cells of leaves after emergence, but albino plants varied in their ability to accumulate starch. The poor ability of some albino plants to accumulate starch may be associated with the observation that not all corn albinos can be successfully cultured on sugar. It was further found that the guard cells of the albino plants accumulated starch from 0.3M sucrose or 0.3M maltose feeding.

The albino cells were also found to react to changes in pH. That externally applied pH changes cause normal guard cells to operate has been reported by Small and coworkers (*29*, *30*), Said and Tolba (*25*), and Tolba (*33*). One-half-centimeter sections of albino leaves were floated in the dark on buffer solutions containing 0.002M sucrose. The sucrose was added because the plants did not have starch uniformly in guard cells throughout a leaf and their ability to operate would probably depend on a starch or sugar substrate. The starch was concentrated near the leaf end immersed for sugar feeding. An acetic acid, sodium acetate buffer, was used. The pH value ranged from 5.0 to 7.0 in 0.2 gradations. The albino guard cells opened uniformly at pH 6.4 only. No definite correlation in the absence of guard cell starch and opening could be found.

The ability of guard cells to open at pH 6.4, plus the frequent observation that a large number of the stomata opened under sugar feeding, implies that the albino guard cells have the ability to operate. This finding was not so important as anticipated, because the paper-white corn plants are not true albinos. Upon subjection to ultraviolet light, a microscopically perceptible red fluorescence occurred in many of the guard cells, indicating the presence of finite amounts of chlorophyll. The silver nitrate test for chlorophyll was also weakly positive, and confirms the presence of chlorophyll.

On the basis of earlier work with albino barley, Ketellapper (*12*) suggested there is no light reaction in guard cells when chlorophyll is not present. This is possibly true, although Heath (*9*) suggests that the light reaction may be mediated by the carotenoids.

The work of Tolba (*33*) indicates that not only a light reaction is taking place in guard cell operation but also another phenomenon. He found opening of guard cells to occur at certain pH values that did not correlate with decreases in guard cell starch. The lack of correlation of guard cell operation with starch content, as indicated by Tolba and this work, is explainable if a protoplasmic change is also responsible for guard cell action. A pH effect on colloidal hydration has already been suggested (Scarth, *27*; Tolba *33*).

A change in the hydration capacity of the protoplasm, possibly by a reorientation of the polypeptide chains, may be partially responsible for stomatal movements; or an expansion of the protoplasm may occur that aids in opening the stomata. Either of these protoplasmic changes would have been included but not necessarily defined in turgor measurements. That a turgor change does take place between the open and the closed condition of the stomata is the one point in stomatal physiology on which all researchers agree.

## STARCH ACCUMULATION IN THE DESTARCHED LEAVES OF PLANTS

Preliminary experimentation (*35*) indicated that guard cell starch in the leaves of normal plants can originate from other than photosynthesis in the guard cell. If this phenomenon was representative of most species of the Angiospermeae, it was not known. It was anticipated that representatives of each order of the Angiospermeae (Benson, *2*) would be destarched and the ability of their guard cells to utilize various sugars be determined in order to establish a possible biochemical pathway of starch production in guard cells.

Germination and culture of test species in total darkness were not found suitable for testing the guard cells of a large number of species. Many of the plants were difficult to work with, as they were malformed and brittle. The procedure adopted was to start plants from seed and to grow corms, tubers, or cuttings in the greenhouse. When mature leaves were available, the plants were transferred to a semidark, diurnal cycle at 30° C. for destarching. Light was supplied during a 12-hour daylight period from a 25-watt incandescent bulb and was approximately 1 ft.-c., as measured by a Weston foot-candle meter. A summary of destarching ability of various plants is found in table 3. The order of listing follows Benson's system of classification (*2*). Some species were difficult to destarch. Figures 14, 15, 16, and 17 are representative of some of the difficult species showing starch in early and late stages of destarching.

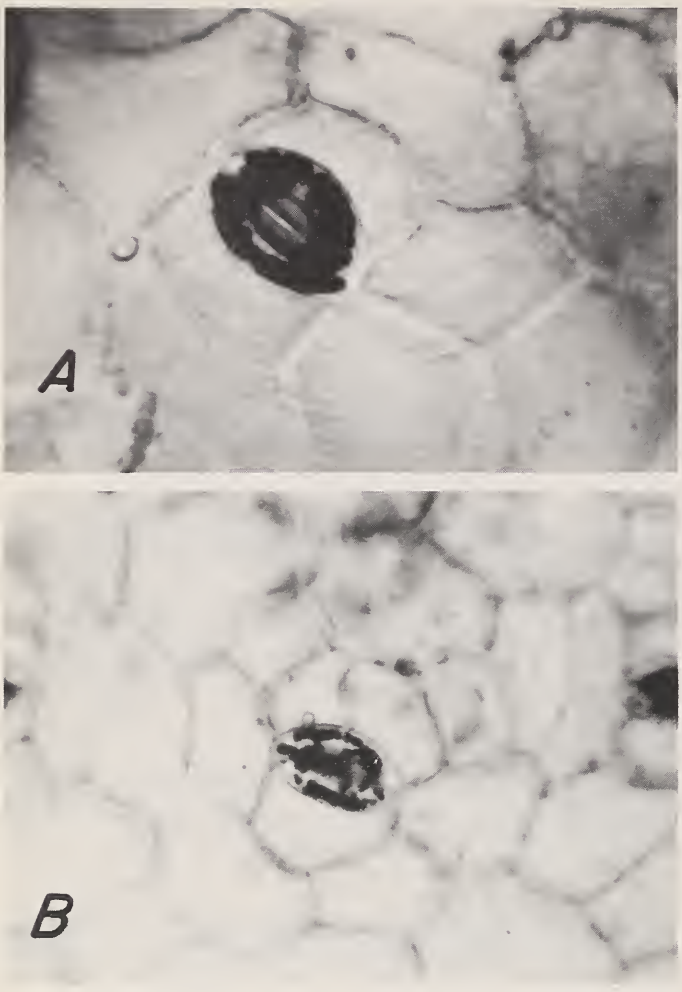


FIGURE 14.—Guard cell starch in calla lily (*Zantedeschia elliottiana*): *A*, Two days after placing in destarching chamber; *B*, after destarching 49 days and immediately preceding death of the leaf.

In general, when reserve substances are available in corms as in calla lily, or woody stems as in crapemyrtle, destarching of the guard cells is difficult. The indication is that as long as reserve substances are available, the guard cells appear to be able to draw on them and, in turn, keep their starch content high. Evidently the ability of guard cells to accumulate and retain starch is quite pronounced; evolutionarily, this may be significant.

To test the ability of guard cells of various species to utilize different sugars, epidermal peelings were made after destarching and floated on sugar solutions contained in small vials placed in a water bath at 30° C. Table 4 summarizes the experimental results. Plants are listed in an order consistent with Benson's classification (*2*).

In initial studies little attention was paid to adhering mesophyll cells, since in many species adhering tissue was impossible to avoid (see table 3). Figure 15 depicts such adherences. However, adhering cells have been found to be active in assimilating sucrose and other sugars leading to starch formation in the guard cells. The mor-

FIGURE 15.—Guard cell starch accumulation in rhubarb (*Rheum rhaponticum*). The dark indefinite areas (see arrow) indicate adhering mesophyll cells. Only proximal to such areas was the test sugar, fructose, accumulated as starch in the guard cells.

FIGURE 16.—Guard cell starch accumulation in periwinkle (*Vinca major*). Ribose conversion to starch occurred only in the vicinity of a vein.

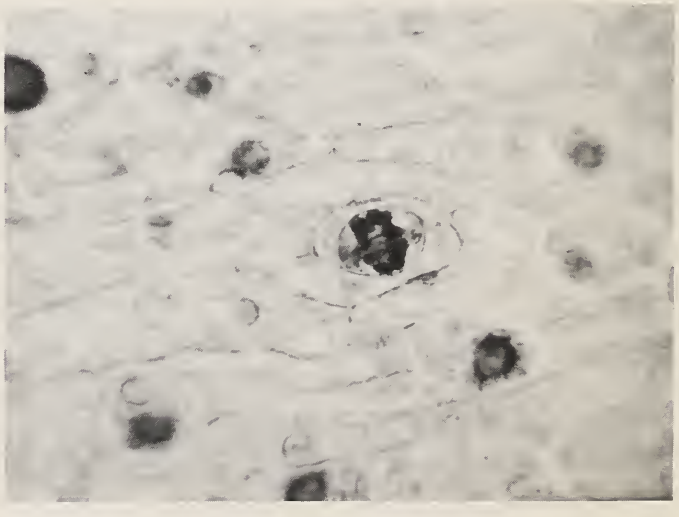

FIGURE 17.—Guard cell starch in cactus (*Opuntia vulgaris*) 6 months after the plant was placed in destarching chamber.

TABLE 3.—*Destarching and usability of various species*

| Genus and species | Number of days to destarch | | Clarity of starch | Amount of starch remaining at death [2] | Usability for guard cell tests | |
|---|---|---|---|---|---|---|
| | Maximum [1] | Minimum | | | Peeling ability | Adhering tissue [2 3] |
| *Liriodendron tulipifera* (poplar) | 20 | 12 | Fair | | Fair | + |
| *Brassica oleracea* var. *acephala* (collards) | 20 | 10 | Good | — | Good | + |
| *Viola papilionacea* var. *priceana* (violet) | (*) | | do | | Poor | ++ |
| *Gossypium hirsutum* (cotton) | 18 | 12 | Fair | | do | ++ |
| *Ricinus communis* (castorbean) | | | Good | — | Fair | + |
| *Tropaeolum majus* (nasturtium) | 14 | 7 | Poor | ± to — | Poor | ++ |
| *Ailanthus altissima* (tree-of-heaven) | 30 | 24 | Good | — | Fair | ± |
| *Melia azedarach* (chinaberry) | 14 | 7 | do | — | do | ± |
| *Parthenocissus quinquefolia* (Virginia creeper) | (*) | | Fair | ± | Poor | ++ |
| *Rosmarinus officinalis* (rosemary) | | | Good | | do | ++ |
| *Capsicum frutescens* var. *grossum* (pepper) | (*) | | do | | Good | ± |
| *Tetragonia expansa* (New Zealand spinach) | | | Fair | | Poor | ++ |
| *Rumex patientia* (dock) | | | Good | — | Good | ± |
| *Rheum rhaponticum* (rhubarb) | 14 | 6 | do | — | do | + |
| *Cyclamen indicum* (cyclamen) | 14 | 12 | do | | do | ± |
| *Diospyros virginiana* (persimmon) | | 14 | Fair | | Poor | ++ |
| *Azalea obtusum* (azalea) | | | do | | do | ++ |
| *Gelsemium sempervirens* (yellow jessamine) | 14 | 7 | do | ± to — | Fair | ++ |
| *Syringa vulgaris* (lilac) | | | do | | do | ++ |
| *Ligustrum vulgare* (privet) | | | do | | Poor | ++ |
| *Fraxinus pennsylvanica* (ash) | 12 | 6 | do | — | do | ++ |
| *Vinca major* (periwinkle) | 21 | 7 | Good | — | Good | ± |
| *Ipomoea purpurea* (morning-glory) | 14 | 7 | do | — | Fair | + |
| *Lycopersicon esculentum* var. *commune* (tomato). | 10 | 6 | do | — | do | ± |
| *Antirrhinum majus* (snapdragon) | 10 | 4 | do | — | Good | ± |
| *Plantago lanceolata* (plantain) | 20 | 7 | Fair | — | Fair | ++ |
| *Bryophyllum pinnatum* (bryophyllum) | (*) | | Good | ± | Good | ± |
| *Phaseolus vulgaris* (bean) | | | do | — | Fair | + |
| *Elaeagnus commutata* (silverberry) | | | Poor | | Poor | ++ |
| *Opuntia vulgaris* (cactus) | [4] (*) | | Fair | ± | Fair | ++ |
| *Lagerstroemia indica* (crapemyrtle) | | | Good | | Poor | ++ |
| *Hedera helix* (ivy) | 21 | 14 | Poor | — | do | ++ |
| *Phoradendron flavescens* (mistletoe) | | | do | | do | ++ |
| *Begonia semperflorens* (begonia) | (*) | | Good | ± | Fair | ± |
| *Cucurbita pepo* var. *condensa* (squash) | 10 | 7 | do | — | do | + |
| *Campanula medium* (Canterbury-bells) | 14 | 6 | do | — | Good | ± |
| *Helianthus annuus* (sunflower) | 12 | 6 | do | — | Poor | ++ |
| *Quercus acuta* (oak) | 20 | 14 | Poor | — | do | + |
| *Zebrina pendula* (wandering Jew) | 14 | 7 | Good | — | Good | ± |
| *Zantedeschia elliottiana* (calla lily) | (*) | | do | ± | Fair | ++ |
| *Zea mays* (corn) | 20 | 10 | Fair | — | Poor | ++ |
| *Canna indica* (canna lily) | 75 | 27 | do | ± to — | Fair | ++ |

[1] *=unable to destarch successfully.

[2] ++=large amount; +=medium amount; ±=small amount; —=none; __=no data available.

[3] Predominantly mesophyll cells.

[4] In 8 months.

phologically different epidermal cells occurring over the veins of some species also exhibit the ability to transform sugars to a form usable by the guard cells, although regular epidermal cells do not have the ability. Figure 16 is an example and shows starch accumulation from ribose found only in guard cells next to veins in *Vinca major.*

Depending on the species, maltose, sucrose, fructose, glucose, galactose, raffinose, and xylose—all may serve as precursors to guard cell starch mediated by cells other than the guard cells. Only glucose-1-phosphate (G-1-P) appears immediately available to the guard cells. This agrees with the work of Ono in Japan (*21*). The accumulated evidence suggests G-1-P is the predominant sugar form translocated to the guard cell and is converted to starch in a one-step reaction, mediated by the enzyme phosphorylase.

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TABLE 4.—*Induced starch accumulation in guard cells of various species that had been destarched (table 3)*

| Order and family | Species | Sugar | Starch [1] accumulation after— | | | | Notes [2] |
|---|---|---|---|---|---|---|---|
| | | | 14 hr. | 24 hr. | 48 hr. | 96 hr. | |
| PAPAVERALES | *Brassica oleracea* var. *acephala* (collards). | Control | -------- | − | − | ------ | |
| Cruciferae. | | 0.3M sucrose | -------- | + | + | ------ | |
| | | Galactose | -------- | + | + to − | ------ | Adhering tissue to no adhering tissue. |
| | | Ribose | -------- | + | + to ± | ------ | Do. |
| | | Raffinose | -------- | + | + | ------ | Do. |
| | | Fructose | -------- | + | + to − | ------ | |
| | | G–1–P [3] | -------- | + | -------- | ------ | No adhering tissue (some cells had no starch but stomata were open). |
| MALVALES | *Gossypium hirsutum* (cotton). | Control | ± | ± | -------- | ------ | |
| Malvaceae. | | 0.3M sucrose | + to − | + to − | -------- | ------ | |
| GERANIALES | *Melia azedarach* (chinaberry). | Control | -------- | − | − | ------ | |
| Meliaceae. | | G–1–P | -------- | + | + | ------ | Possible adhering tissue. |
| | | 0.3M sucrose | -------- | − | − | ------ | |
| RUTALES | *Ailanthus altissima* (tree-of-heaven). | Control | -------- | − | -------- | ------ | |
| Simaroubaceae. | | 0.3M sucrose | -------- | − to + | -------- | ------ | Near leaf section. |
| | | 0.02M G–1–P | -------- | + | -------- | ------ | No adhering tissue. |
| CARYOPHYLIALES | *Rheum rhaponticum* (rhubarb). | Control | -------- | − | − | ------ | |
| Polygonaceae. | | 0.3M sucrose | -------- | + | + to − | ------ | |
| | | Galactose | -------- | + | + | ------ | |
| | | Xylose | -------- | -------- | + | ------ | |
| | | Raffinose | -------- | -------- | + | ------ | |
| | | Maltose | -------- | -------- | + to ± | ------ | |
| | | Mannose | -------- | -------- | − | ------ | |
| | | G–1–P | -------- | + | − | ------ | Adhering tissue; open stomata 50 to 75 percent. |
| APOCYNALES | *Vinca major* (periwinkle). | Control | ± | ± to − | -------- | ± | |
| Apocynaceae. | | 0.3M sucrose | + | + | -------- | ± | |
| | | Maltose | + | ± | -------- | ------ | |
| | | Fructose | − | ± to − | -------- | ------ | |
| | | Glucose | − | ± to − | -------- | ------ | |
| | | Glucuronic acid | -------- | ± | -------- | ------ | |
| SCROPHULARIALES. | *Antirrhinum majus* (snapdragon). | Control | -------- | − | − | ------ | |
| Scrophulariaceae. | | 0.3M sucrose | -------- | − | − | ------ | No adhering tissue. |
| | | 0.03M sucrose | -------- | − | − | ------ | Do. |
| | | G–1–P | -------- | − | + | ------ | Do. |
| PLANTAGINALES | *Plantago lanceolata* (plantain). | Control | -------- | − | -------- | ------ | |
| Plantaginaceae. | | 0.3M sucrose | -------- | + | -------- | ------ | |
| | | G–1–P | -------- | − | -------- | ------ | |
| ROSALES | *Phaseolus vulgaris* (bean). | Control | -------- | ± | ± | ------ | |
| Leguminosae. | | 0.3M sucrose | -------- | + | + | ------ | |
| | | Fructose | -------- | + | + | ------ | |
| | | Glucose | -------- | + | + | ------ | |
| | | Maltose | -------- | + | + | ------ | |
| CACTALES | *Opuntia vulgaris* (cactus). | Control | -------- | ± | ± | ------ | |
| Cactaceae. | | 0.3M sucrose | -------- | + | + | ------ | |
| UMBELIALES | *Hedera helix* (ivy). | Control | -------- | − | − | ------ | |
| Araliaceae. | | 0.3M sucrose | -------- | + | -------- | ------ | |
| | | Glucose | -------- | + | -------- | ------ | |
| | | Galactose | -------- | + | + | ------ | |
| | | Xylose | -------- | + | -------- | ------ | Over adhering tissue. |
| CAMPANULALES | *Campanula medium* (Canterbury-bells). | Control | -------- | − | ± | ------ | |
| Campanulaceae. | | 0.3M sucrose | -------- | + | + | ------ | |
| ASTERAILES | *Helianthus annuus* (sunflower). | Control | ± | ± | -------- | ------ | Stomata open. |
| Compositae. | | 0.3M sucrose | + | + | -------- | ------ | |

See footnotes at end of table.

TABLE 4.—*Induced starch accumulation in guard cells of various species that had been destarched (table 3)*—Continued

| Order and family | Species | Sugar | Starch [1] accumulation after— | | | | Notes [2] |
|---|---|---|---|---|---|---|---|
| | | | 14 hr. | 24 hr. | 48 hr. | 96 hr. | |
| LILIALES | *Allium cepa* (onion). | Control | | — | — | | Onion plasmolized or died (both control and sucrose). |
| Liliaceae. | | 0.3M sucrose | | — | — | | |
| | | 0.03M sucrose | | — | — | | |
| COMMELINALES | *Zebrina pendula* (wandering Jew). | Control | ± | ± | | | |
| Commelinaceae. | | 0.3M sucrose | + | + | | | No visible adhering tissue. |
| MUSALES | *Canna indica* (canna lily). | Control | | ± | ± | | |
| Cannaceae. | | 0.3M sucrose | | + | + | | Possible adhering tissue. |

[1] + = positive increase of starch as compared to control.
± = starch present in small amounts.
— = no starch present.

[2] Adhering tissue was present unless otherwise noted.
[3] Glucose-1-phosphate.

## OSMOTIC PRESSURE DETERMINATIONS

It is generally agreed that the opening and closing movements exhibited by guard cells are the result of a change of turgor in the cells. The change is regarded as being dependent upon a starch-sugar equilibrium. The supporting evidence for such a change at present resides mainly in determinations of the osmotic pressure of guard cells in various species throughout a 24-hour cycle (*31*). The osmotic pressure in guard cells is regarded as rising during the day and falling at night. The actual proof of a starch to sugar equilibrium existing in the guard cells is subject to criticism; other than the indirect evidence from osmotic pressure evaluations, only three reports of guard cell sugar determinations have been found. Rosing (*24*), in 1908, stated that in testing for reducing sugars it was not possible to determine any difference in the amount of sugar in either open or closed stomata. However, Sayre (*26*) came to the conclusion in testing for reducing sugar that there was twice as much sugar in guard cells during the day as at night. Yemm and Willis (*37*) found a correlation of stomatal closure and starch content but no correlation with sugar.

Since Sayre is the only one substantiating a starch to sugar equilibrium, a re-evaluation of his work was undertaken by following the same procedure he outlined, with possibly more attention paid to exactness of the experimental conditions. The plants were grown and maintained in growth chambers under conditions similar to that for the growth of bean plants (p. 5). The same species was used, *Rumex patienta*, as in the original work. Reducing sugar in guard and epidermal cells was determined with Fehling solution every 2 hours for as long as 36 hours.

The conclusion was that although the guard cells opened and closed, no correlation of operation with reducing sugar could be found. This contrary finding led to a check of the diurnal changes in the osmotic pressure of a native species, *Erigeron philadelphicus*, by means of the incipient plasmolysis method (*6*). A drop in osmotic pressure during midday was found, although no change in the stomatal opening was noted. This drop was contrary to most cited results, as in Meyer and Anderson (*19, p. 151*), but was not contrary to Steinberger's findings (*32*). She reported that a midday drop in osmotic pressure often occurred during the noon hours of warm summer days, which she considered was indirectly responsible for the midday depression of transpiration.

## AMYLASE EXPERIMENTS

Hagan (*8*) reported he was able to open artificially the guard cells of *Peperomea mormorate* by submerging leaf pieces in a concentrated solution of diastase, which we now recognize as having contained $\alpha$ and $\beta$ amylase. It is pertinent to the theory of guard cell action, as well as economically important, if $\alpha$ and/or $\beta$ amylase have the ability to open guard cells. An amylase-like enzyme was earlier postulated (*13*) to exist in guard cells, although it has never been isolated.

Experiments were conducted to test the effect of amylase solutions on the guard cell activity of several species.

*Experiment 1.*—Leaf disks from the mature leaves of *Phaseolus vulgaris* were placed in vials containing 1,000, 10, or 0.1 p.p.m. $\alpha$ amylase in distilled water, $\beta$ amylase in distilled water, $\alpha$ amylase and 0.01 percent Nonic 218 (polyethylene

glycol tertdodecyl thioether), $\beta$ amylase and 0.1 percent Nonic 218, distilled water, or 0.1 percent Nonic. Prior to placement, the stomata were checked to make sure they were closed and an estimate of guard cell starch was made for later comparative purposes. The condition of the stomata was observed 2½, 14, and 26 hours after treatment.

More stomata opened, and wider openings were observed, in either 1,000 p.p.m. $\alpha$ or $\beta$ amylase. With decreasing amylase concentration, stomatal opening resembled that found in the 0.1 percent Nonic 218. More stomata were open in Nonic than in distilled water. Epidermal strips containing guard cells floated on water have been reported to open, possibly a reflection of passive movements discussed in a preceding subsection (p. 18). Fourteen hours later, all stomata were found to have closed to some extent. At this time starch had disappeared in all but those guard cells subjected to the lowest concentration of amylase or in distilled water.

It was unknown why guard cell starch disappeared in 0.1 percent Nonic 218. It had originally been included in this experiment to increase wetting. The experimental results with amylase could not be evaluated until further information on Nonic action was available.

*Experiment 2.*—This experiment utilized the same solutions as experiment 1, but leaf disks were taken from the mature leaves of *Zea mays*. The condition of stomata was observed at 2 and 4 hours after treatment, and starch content in guard cells was determined after 24 hours.

None of the treatments unequivocally opened the stomata of corn. A few were opened in $\alpha$ amylase at 1,000 or 10 p.p.m. when checked at the 4-hour period, but the area of opening was correlated with a translucent appearance of the leaf at that point.

The 24-hour starch check showed a normal starch accumulation in the distilled water control and 0.1 p.p.m. $\alpha$ amylase. Guard cells treated with 1,000 p.p.m. and 10 p.p.m. $\alpha$ amylase and with Nonic 218 lacked starch.

*Experiment 3.*—Several wetting agents were included in this experiment to test their effect on guard cell activity. Leaf disks of bean leaves were submerged in three wetting agents; namely, 0.1 and 0.01 percent Tween 20 (polyoxyethylene glycol sorbiton monolaurate), Nonic 218, or Vatsol OT (sodium dioctylsulfosuccinate). The stomatal condition of these disks were checked 4, 7, and 27 hours later. Four hours after treatment, stomata in all treatments opened, but the opening occurred between the time the epidermis was stripped from disks and observed through the microscope. Seven hours after treatment, the condition of the stomata was observed without peeling. That the stomata opened after peeling was reconfirmed; open stomata in leaf disks were found only at the edge of disks or in thoroughly wetted translucent areas. One-tenth percent Vatsol OT and Nonic 218 were evidently toxic, as coagulation of protoplasm was noted in some treated guard cells. The disappearance of starch in Nonic-treated guard cells in the previous experiment probably was caused by Nonic toxicity.

*Experiment 4.*—Since Hagen (*8*) reported he had to evacuate the tissue to facilitate opening of the stomata by diastase, it was surmised that penetration of the enzyme molecule was limiting amylase action. The lack of starch in the guard cells at the end of experiments 1 and 2 indicated a degradation of the starch. However, the degradation, if limited by enzyme concentration, could have been too slow to have had an observable effect on guard cell activity, or possibly the degradation products could have diffused out of the cell without an effect on stomatal condition. An attempt was made to increase the penetration of amylase into the guard cells.

It has been reported that ethyl alcohol as well as acetone increases the cellular penetration of some substances.[8] Various mixtures of alcohol and acetone were tried. Whether alcohol or acetone had any effect on $\alpha$ or $\beta$ amylase activity was determined by following cornstarch digestion at various concentrations of enzyme in vitro. High concentrations of alcohol or acetone mixed with distilled water (50 percent by volume) interfered with the color reaction necessary for evaluation of amylase enzyme activity. A 25-percent or less alcohol or acetone solution had no apparent effect on the activity of the enzymes.

Concentrations of $\alpha$ and/or $\beta$ amylase at 500 and 5 p.p.m. were used in solutions of 25 and 12.5 percent acetone or ethyl alcohol, or in solutions of 1,000 p.p.m. Tween 20, Nonic 218, or Vatsol OT. With the same proportions maintained, all combinations of amylases, acetone, alcohol, and wetting agents were used also. The solutions were checked for stomatal effect by submerging leaf disks in well slides containing a solution or by applying a drop of solution directly on a mature leaf. The stomata were observed 60 minutes after application. *Zea mays*, *Zebrina pendula*, *Lycopersicon esculentum* var. *commune*, *Brassica rapa*, and *Nicotiana tabacum* were the species tested. Prior to use, all plants were placed in the dark to close stomata, after which the guard cells were stained with iodine-potassium iodide to insure that starch was present.

No reproducible effect by the amylase solutions was found in any of the species tested.

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[8] Pallas, J. E., Jr. Effects of temperature and humidity on the absorption and translocation of 2,4-dichlorophenoxyacetic acid and benzoic acid. 1958. (Unpublished dissertation; on file at University of California, Davis.)

## FUTURE STUDIES

Much remains to be studied before we can understand stomatal action on the cellular level. Further investigations of the changes in osmotic pressure effects are necessary, especially as the changes are related to environment. The isolation and characterization of the enzyme or enzymes responsible for guard cell starch degradation is a worthwhile project, but probably a very difficult task. Studies on sugar feeding should be continued.

# EFFECTS OF CERTAIN CHEMICALS ON TRANSPIRATION

Transpiration does not appear to be a biologically efficient process, since less than 5 percent of the soil water transpired is incorporated in the constitution of the plant (*15*). The eventual control of transpiration is a goal worth attaining, whether the results would be to increase or decrease its efficiency. For example, chaos would result if stomata of crops were forced open by minute quantities of spray and would result in withering and death of plants. A decided advantage would be obtained in offensive or defensive movements if an army had control of ground environment, as might be possible by controlling transpiration.

The production of crops by hydroponics in time of war has already proved itself militarily worthwhile. After a nuclear holocaust, such production might be the only safe, feasible method of crop production in certain areas of the world. It allows man to control the removal of radioactive contaminants. The methods of decontamination would be laborious and costly; therefore, increased efficiency of use of any of the components making up the system would be important. There are many other examples that one could cite for this project, but let us focus our attention on what has been accomplished by other workers to date.

The first growth regulator discovered, indoleacetic acid, was found to have no effect on the stomatal aperture of *Sinapsis alba* and *Sambucus nigra* (*3*). That it had no direct effect on stomata was verified by Johansen (*11*). Brown (*5*) reported a 34-percent decrease in the transpiration of bean seedlings when sprayed with 1,000 p.p.m. 2,4–D. The compound was found to be lethal at that concentration. In 1949 (*7*) and in 1952 (*4*), 2,4–D and $\beta$-naphthoxyacetic acid were reported to close stomata at least partially, thus decreasing transpiration.

Player (*22*) used two replications of either corn or castorbean plants and found no change in the transpiration of corn sprayed with indole-3-acetic acid, $\beta$-naphthoxyacetic acid, P-chlorophenoxyacetic acid, 2,4–D, $\beta$ (indole-3)-propionic acid, or $\gamma$ (indole-3) butyric acid at two concentrations. However, significant reductions in the transpiration of castorbean plants were found, but these reductions were correlated with toxicity of the acids employed.

Growth regulators, if effective in limiting transpiration, would be considered to exert their control on the enzymatic operation of the guard cells, or possibly to increase cellular resistance to water loss. A coating on the plant, however, whether it be plastic, latex, or a chemical with hygroscopic properties, would exert its greatest influence as a physical barrier to water movement. Barr (*1*) in 1945 reported no ideal transpiration-suppressing compound had been found. Chemicals in the above categories that have given evidence of being useful in transpirational control are tested under a limited screening program. The procedure used to grow plants prior to treatment remains relatively constant and is herewith described. Any deviations will be noted under the specific compounds.

The seed of Red Kidney beans or Dixie 82 corn, the test plants, were germinated in vermiculite in a dark chamber at 30° C. After a 24-hour germination period, seedlings were selected on the basis of root length to insure a uniform population. Each seedling was then planted in a container of 2,000 grams of soil, fertilized at the rate of 4,000 pounds of 4–12–12 per acre, and subirrigated until the soil was uniformly moist. The seedlings were then placed in a growth chamber at 30° for corn, or 25° for beans.

After emergence the bean population was run on a diurnal cycle of 25° C. day temperature, 15° night temperature, and a 14-hour light period provided from the incandescent-fluorescent source mentioned in an earlier subsection (p. 5). The corn was grown under the same light conditions, but the temperature was changed to 30° day temperature and 15° at night.

After 3 weeks of growth, transpiration measurements were made daily for an 8½-hour period by weighing the plants at 0800 and 1630. A plastic cover on the can eliminated soil moisture evaporation. The plants were subirrigated at night for 4 or 5 hours. Transpiration measurements were made for several days prior to treatment. After this the plants were grouped for treatment so that each group used approximately the same amount of water. Five to six plants per treatment was

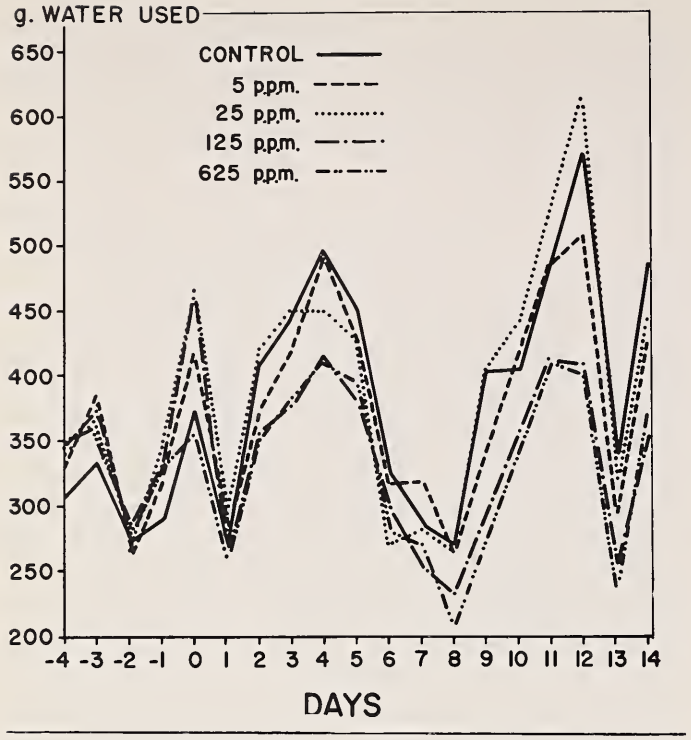


FIGURE 18.—Transpiration of Red Kidney bean plants sprayed at indicated concentrations with β-naphthoxyacetic acid.

standard. Spraying was accomplished with a chromatographic atomizer. Each plant was sprayed until runoff. Results and other pertinent data are included in the following sections.

## 2,4–D

It was reported (*35*) that the decrease in transpiration by various concentrations of 2,4–D sprayed on bean plants was correlated with toxicity. The effect of 5, 25, 125, and 625 p.p.m. of 2,4–D as the triethylamine salt on the transpiration of corn was checked. No significant effect on transpiration was found.

FIGURE 19.—White areas (see arrow) indicate root development along the stem of Red Kidney bean plants when treated with 625 p.p.m. β-naphthoxyacetic acid.

## β-NAPHTHOXYACETIC ACID

An indication (*35*) of some decrease in the transpiration of beans by β-naphthoxyacetic acid was reported. However, a rerun (fig. 18) showed very little difference except for a noticeable decrease in water usage (approximately 15 percent) the fourth day by those plants treated at 625 and 125 p.p.m. Their water usage remained low, but morphological abnormalities developed from the test compound (fig. 19).

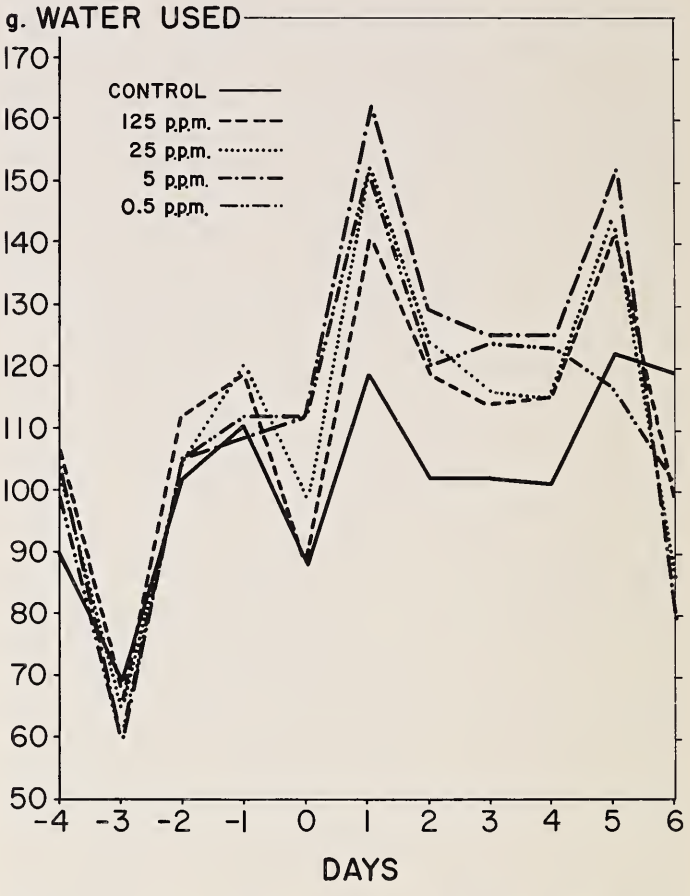


FIGURE 20.—Transpiration of Red Kidney bean plants sprayed at indicated concentrations with $N^6$ benzyladenine.

## $N^6$ BENZYLADENINE

An article in the *Farm Journal* (November 1960) reported that this kinin-like compound increased the storage potential of certain crops several days, and implied that its major effect was to decrease the water lost by its tissues. The compound, $N^6$ benzyladenine, is primarily a senescent inhibitor (*20*).

In the first experiment it was applied at 0, 0.5, 5, 25, and 125 p.p.m. as an aqueous spray on bean plants. As can be seen in figure 20, no noticeable decrease in transpiration is evident. For several days after treatment, the control used less water than the treated plants.

Lack of penetration of the compound could explain the negative results; therefore, a new bean plant population was grown in nutrient culture and the compound was added to the nutrient solution. In general, it did reduce transpiration (fig. 21), but it was toxic at 10 p.p.m., where the greatest effect was noted. A corn population sprayed with $N^6$ benzyladenine and resprayed 5 days later with $N^6$ benzyladenine plus 0.05 percent Vatsol OT as a wetting agent showed no effect by the compound on transpiration rates.

The Shell Development Co. has reported [9] that the compound increased moisture storage in turnips. The results from a population of turnips (fig. 22) that was sprayed showed a decrease in transpiration on the day of spraying for the highest concentration used—about an 8-percent decrease as compared to the control. A respraying of the same concentrations was deleterious to the plant growth, causing a yellowing of leaves at the higher concentrations.

[9] Shell Development Co. SD 4901, AN EXPERIMENTAL SENESENCE INHIBITOR FOR GREEN LEAFY VEGETABLES. Mimeo. Release ARD-60-2. Modesto, Calif. 1960.

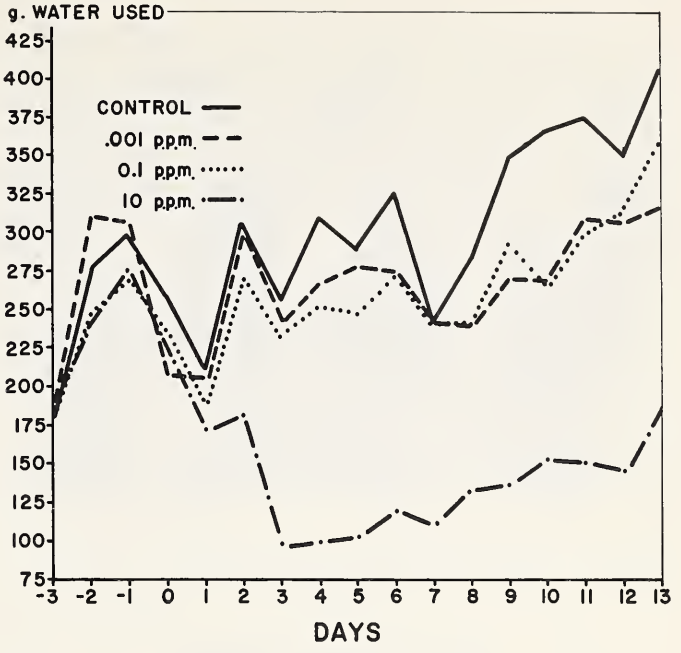


FIGURE 21.—Transpiration of nutrient-cultured Red Kidney bean plants as affected by the addition of $N^6$ benzyladenine to the nutrient solution at indicated concentrations.

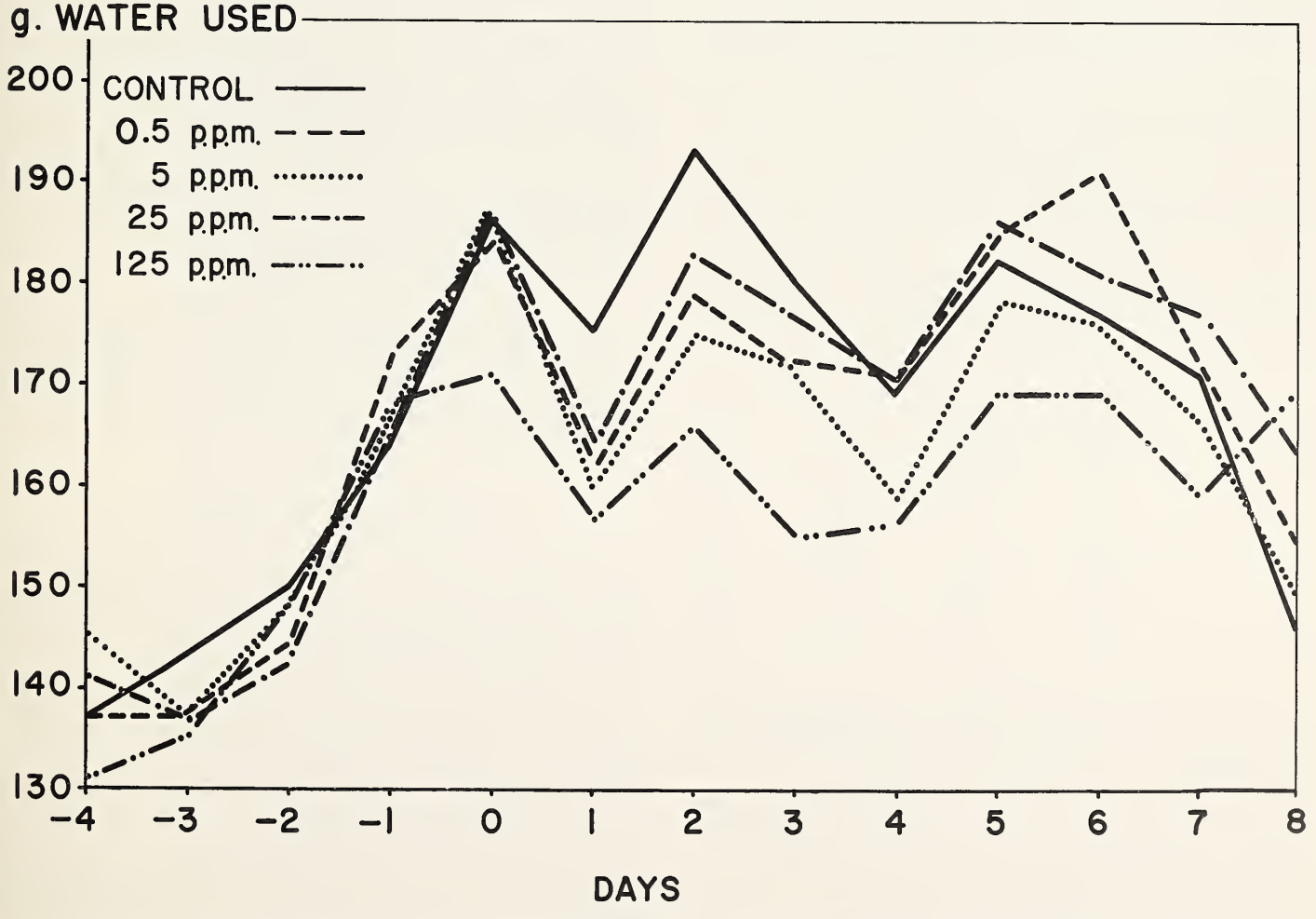


FIGURE 22.—Transpiration of turnip plants sprayed at indicated concentrations with $N^6$ benzyladenine.

FIGURE 23.—Plants sprayed with hexadecanol (left to right): Control, 0.01, 0.1, and 1 percent, respectively.

## HEXADECANOL

Roberts [10] reported that application of hexadecanol increased the efficiency of water usage in a field of corn. Woolley (*36*) reported no increase in efficiency of water use by corn plants growing in soil treated with hexadecanol.

The compound was tested in a spray solution. Since hexadecanol was only slightly soluble in water, 90 percent ethyl alcohol had to be used as a solvent. It was tested at 1, 0.1, and 0.01 percent by weight on both corn and bean plants. Control plants were sprayed with 90 percent ethanol.

Tables 5 and 6 show the results of the experiment, and figure 23 depicts the phytotoxicity observed on beans at the higher concentration. The spray was not considered to reduce significantly transpiration of those plants tested without affecting growth.

TABLE 5.—*Effect of hexadecanol on bean transpiration*

| Days [1] | Water used by plants for each treatment [2] | | | |
|---|---|---|---|---|
| | Control | 0.01 percent | 0.1 percent | 1 percent |
| | *Grams* | *Grams* | *Grams* | *Grams* |
| −5 | 121 | 125 | 122 | 124 |
| −4 | 126 | 128 | 130 | 138 |
| −3 | 143 | 142 | 149 | 141 |
| −2 | 119 | 125 | 123 | 119 |
| −1 | 129 | 129 | 135 | 148 |
| 0 | 151 | 168 | 158 | 67 |
| 1 | 131 | 128 | 130 | [3] 88 |
| 2 | 130 | 127 | 140 | [3] 98 |
| 3 | 128 | 134 | 132 | [3] 100 |
| 4 | 138 | 139 | 142 | [3] 118 |
| 5 | 108 | 116 | 108 | 106 |

[1] The minus-numbered days represent days of transpiration measurements before treatment, 0 represents the treatment day, and the remaining numbers represent days after treatment.

[2] Treatments: Control plants sprayed with 90-percent ethanol; hexadecanol sprayed at rate of 1, 0.1, and 0.01 percent by weight.

[3] Reduction in transpiration due to phytotoxicity.

TABLE 6.—*Effect of hexadecanol on corn transpiration*

| Days [1] | Water used by plants for each treatment [2] | | | |
|---|---|---|---|---|
| | Control | 0.01 percent | 0.1 percent | 1 percent |
| | *Grams* | *Grams* | *Grams* | *Grams* |
| −6 | 136 | 148 | 137 | 132 |
| −5 | 149 | 160 | 135 | 149 |
| −4 | 164 | 156 | 161 | 166 |
| −3 | 146 | 138 | 140 | 156 |
| −2 | 182 | 182 | 170 | 169 |
| −1 | 160 | 162 | 155 | 141 |
| 0 | 113 | 129 | 104 | 87 |
| 1 | 163 | 179 | 165 | 168 |
| 2 | 124 | 133 | 163 | 128 |
| 3 | 152 | 133 | 122 | 126 |
| 4 | 190 | 178 | 176 | 181 |

[1] The minus-numbered days represent days of transpiration measurements before treatment, 0 represents the treatment day, and the remaining numbers represent days after treatment.

[2] Treatments: Control plants sprayed with 90-percent ethanol; hexadecanol sprayed at rate of 1, 0.1, and 0.01 percent by weight.

## CARBOWAX

Carbowax is reported to have outstanding humectant properties. No decrease in the transpiration of bean plants was found when they were sprayed with Carbowax 6000 or 600 at 1.0, 0.1, or 0.01 percent water solutions.

## FUTURE STUDIES

Testing will be continued of compounds that offer some potential in suppressing transpiration. Several commercially available products remain to be tested and include Wilt-Pruf, Rutex, Sun Oil Wax, Vanex, Latex 5229, and Latex 5230.

A polyethylene formulation could be an ideal compound for transpiration control because of its imperviousness to water and permeability to oxygen and carbon dioxide. Several formulations will be tested as foliar sprays.

It is anticipated that the cellular studies will eventually lead to an understanding of the biochemical sequences taking place in the guard cell so that by metabolic blocks it will be possible to control guard cell action and transpiration.

[10] ROBERTS, W. J. REDUCING TRANSPIRATION FROM PLANTS. Soil Conserv. Soc. Amer. Proc., 16th Ann. Meeting, 8 pp. 1961. [Mimeographed.]

## SUMMARY

Prediction equations for transpiration have been developed from an extensive study of one species at the Southern Piedmont Field Station, Watkinsville, Ga. The limitations of the equations are discussed. Approximately 80 percent of the transpiration can be accounted for; however, it is anticipated that through more precise monitoring the reliability can be increased.

Studies on other species that emphasize the effect of soil moisture tension on transpiration have been completed.

Several cellular studies indicate that guard cells have the extraordinary ability to remain operative under extremely adverse conditions. Thus, the importance of guard cell action assumes new proportions. The induction of guard cell operation in vitro can be shown but not completely controlled. It is evident that photoactive and hydroactive movements occur, but much more remains to be learned of their interdependence and independence.

The pathway of guard cell starch accumulation has been partially elucidated. The mechanism(s) of starch breakdown in the guard cell is little understood.

The effects of five compounds as foliar sprays on the transpiration of several species are reported. No tested compound was outstanding in suppressing transpiration.

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